Volume LXXIII Number 6

THE BOTANICAL GAZETTE

Editor: JOHN M. COULTER

JUNE 1922

Variation in Cytology and Gross Morphology of Taraxacum. Contributions from the Hull Botanical Laboratory 295 - Paul Bigelow Sears 425
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(With seven figures)

Overwintering of Tomato Mosaic Max W. Gardner and James B. Kendrick 469
(With Plate XVII)

Stroma and Formation of Perithecia in Hypoxylon. Contributions from the Hull Botanical Laboratory 296 - - - - - Patsy Lupo 486
(With Plate XVIII and seven figures)

Current Literature

Notes for Students - - - - - - - - - - - 496

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A MONTHLY JOURNAL EMBRACING ALL DEPARTMENTS OF BOTANICAL SCIENCE

EDITED BY

JOHN M. COULTER

With the assistance of other members of the botanical staff of the University of Chicago

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TABLE OF CONTENTS

		PAGE
Nonsymbiotic germination of orchid seeds (with three figures)	*Lewis Knudson*	1
Yellow-white pine formation at Little Manistee, Michigan (with six figures)	*LeRoy H. Harvey*	26
Formulas for calculating number of fruits required for adequate sample for analysis	*F. E. Denny*	44
Uredinales collected by R. Thaxter and J. B. Rorer in Trinidad (with four figures)	*J. C. Arthur*	58
Classification of the anaerobic bacteria	*Hilda H. Heller*	70
Sulphur as a factor in soil fertility. Contributions from the Hull Botanical Laboratory 289	*John Woodard*	81
Cyclic manifestation of sterility in *Brassica pekinensis* and *B. chinensis* (with seven figures)	*A. B. Stout*	110
The peltate Peperomias of North America (with plates I–IV)	*William Trelease*	133
Flowers and insects. XXI. Data of anthecology	*Charles Robertson*	148
Influence of salts on bacterial activities of soil	*J. E. Greaves*	161
Vascular anatomy of *Angiopteris evecta*. Contributions from the Hull Botanical Laboratory 290 (with plates V–VIII and eight figures)	*Hugo L. Blomquist*	181
Symbiosis in a deciduous forest. I (with three figures)	*W. B. McDougall*	200
Effect of temperature on germination of *Amaranthus retroflexus*. Contributions from the Hull Botanical Laboratory 291 (with four figures)	*Clytee R. Evans*	213
Nitrogen fixation in Ericaceae (with four figures)	*M. Cheveley Rayner*	226

PAGE

Rhizophidium polysiphoniae in the United States. Contributions from the Hull Botanical Laboratory **292** (with ten figures) - - - - - *George W. Martin* 236

Developmental selection in vascular plants (with twenty-eight figures) - - - - - - *John T. Buchholz* 249

Biochemistry of plant diseases (with seven figures) *J. J. Willaman* and *W. M. Sandstrom* 287

Variations in cytology and gross morphology of *Taraxacum*. I. Contributions from the Hull Botanical Laboratory **293** (with plates IX, X) *Paul B. Sears* 308

Annularia with *Paleostachya* fruit (with two figures) - - - - - - - - - - *Eda M. Round* 326

Cytology of chlorophyll types of maize (with plates XI–XVI) - - - - - - - - - *L. F. Randolph* 337

Cultivation of excised root tips and stem tips under sterile conditions (with four figures) - - *Wm. J. Robbins* 376

Influence of wheat seedlings upon the hydrogen ion concentration of nutrient solutions - - *Linus H. Jones* and *John W. Shive* 391

Sulphur and nitrogen content of alfalfa grown under various conditions. Contributions from the Hull Botanical Laboratory **294** - - - *E. H. Hall* 401

Variation in cytology and gross morphology of *Taraxacum*. II. Contributions from the Hull Botanical Laboratory **295** (with nine figures) - *Paul B. Sears* 425

Anatomy of *Equisetum giganteum* (with seven figures) - - - - - - - - - *Isabel M. P. Browne* 447

Overwintering of tomato mosaic (with plate XVII) *Max W. Gardner* and *James B. Kendrick* 469

Stroma and formation of perithecia in *Hypoxylon*. Contributions from the Hull Botanical Laboratory **296** (with plate XVIII and seven figures) *Patsy Lupo* 486

PAGE

CURRENT LITERATURE - - - - - - - 80, 153, 239, 329, 412, 496

For titles of book reviews see index under author's name and reviews

Papers noticed in "Notes for Students" are indexed under author's name and subjects

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ERRATA

VOL. LXXII

P. 341, line 5, omit sweet pea

P. 372, line 4 from bottom, for most read moist

VOL. LXXIII

P. 62, lines 3 to 5, delete sentence referring the Brazilian rust on *Lygodium* to the genus *Desmella*

P. 85, line 4 from bottom, for LIPMAN read LIPMAN and GERICKE

P. 87, line 8, for ROBINSON (**59**, **60**) read ROBINSON (**59**) and ROBINSON, STEINKONIG, and FRY (**60**)

P. 201, line 2 from bottom, for following read preceding

P. 223, Fig. 3, for 1.19 read 11.9

P. 278, line 10 from bottom, for equal read comparable

P. 285, line 2 under Literature Cited, for Am. So. read Ann. Sci.

P. 382, Table III, last column, for 0.1240 read 0.0240

P. 383, Fig. 3 is inverted, making the legend incorrect as to right and left

NOTICE

With the close of the present volume of the *Botanical Gazette*, a new arrangement for publication will go into effect. The total number of pages published annually will not be diminished, but each volume will contain four numbers of at least 120 pages each. The months omitted in publication will be July and August, and January and February.

VOLUME LXXIII NUMBER 6

THE

BOTANICAL GAZETTE

June 1922

VARIATIONS IN CYTOLOGY AND GROSS MORPHOLOGY OF TARAXACUM

II. SENESCENCE, REJUVENESCENCE, AND LEAF VARIATION IN TARAXACUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY **295**

PAUL BIGELOW SEARS

(WITH NINE FIGURES)

The variability of *Taraxacum* has frequently been recorded in botanical literature without receiving much elucidation. It is less often an object of investigation than of conjecture and discussion. A few botanists have studied the effect of environmental factors upon *Taraxacum*, but their results have not cleared away taxonomic difficulties. Systematic botanists have either looked upon the variations in this genus as fluctuations or slight mutations, and then proceeded to lump or split as judgment might dictate. That life history exerts a profound influence upon form seems generally to have escaped attention.

The 1910 supplement of *Index Kewensis* (**12**) lists 152 new species as described within five years, mainly from Scandinavia. Leaving aside such overwhelming evidence of polymorphy, it is interesting to note that the painstaking monograph of HANDEL-MAZETTI (**10**) admits fifty-seven species. These fall into eleven sections. Of these eleven sections four are so distinctive that none of their species have been mistaken by preceding students for either *T. vulgare* or *T. laevigatum*. In each of the remaining sections species have

been confused at various times with one or the other of the familiar species named, and designated accordingly in publications. Beyond question some of this confusion has been due to bad taxonomy. There is ample reason to believe that more of it has been caused by lack of definite boundaries between species.

Although the two common species mentioned are parthenogenetic, sexual species are known and hybrids may exist. Aside from this possibility, any explanations offered for the overlap between species have been so admittedly hypothetical (**10**) that they need not be rehearsed at this point. It is necessary, however, to take inventory of the precise information available with respect to variation in *Taraxacum* and its causes. It is also necessary to examine the nature of the criteria used in differentiating species and species groups.

ROOT.—Generally referred to as perennial, without modification, it has long been known to branch multicipitally (**4**), and to split into separate individuals (**5**).

STEM.—Usually represented only by a growing point; in the absence of light internodes develop (**20**), giving rise to a vertical rhizome (cf. fig. 4).

LEAVES.—Although taxonomists admit great variability and the frequency of overlap between leaf characters of different species, it is a fact that leaf characters are extensively used in species descriptions and often in distinctions. "Habit" as indicated by leaf orientation is also so used (**3**), despite a lack of evidence that the light responses of *Taraxacum* differ from those of other plants. In a saturated atmosphere greatly elongated leaves are produced (**20**). The reverse is true, that dry air shortens the longitudinal components of the leaf, although WIESNER'S statement that it slightly increases dissection is open to question. Arctic alpine conditions result in a symmetrical dwarfing of the leaves of transplants (**2**). Check and transplant in this experiment were of equal age, and show little difference in degree of leaf dissection in BONNIER'S original figures. Salt itself is not the direct cause of succulence in leaves of saline soil species of *Taraxacum* (**11**). The rate of production of leaves in plants of identical age varies with the habitat, being less in strong sunlight than in shade (**20**).

HANDEL-MAZETTI (10) notes a marked difference in the rate at which oldest leaves die away and leave their bases, considering it a specific characteristic.

As to segmentation, GOEBEL (9) classifies *Taraxacum* with those plants which produce first entire, then dissected leaves, but quotes evidence that segmentation is "richer" in temperate than arctic forms, and in "well-nourished" plants than in "half-starved" meadow-moor forms. DEVARIGNY, as quoted by MORGAN (14), places his own construction upon the matter by attributing the dissection to dry soil conditions and entire leaves to hydrophytic environment. FRANK (8) states that leaf development is basipetal, the tip segment developing first. STORK (17) found that uniform culture conditions upon seedlings (of identical age) produce rather uniform leaf type, regardless of leaf form extremes in the parents.

SCAPE.—The normal course of changes in length and position throughout flowering and fruiting are well known (15). FRANK states that in alpine species the scape is longer in crevice plants than in those growing exposed.

INFLORESCENCE.—Fasciation is admittedly a nonheritable character, and was determined by SCHORBATOW (16) to be due to mechanical pressure during the period of most active flowering, "the third year."

BRACTS.—In taxonomic works these rank highly as criteria, the characteristics used being number, color, size, form, and position. Nevertheless, considerable variability is admitted. HANDEL-MAZETTI notes that infection by *Synchitrium taraxaci* converted the outer bracts of *T. vulgare* into those typical for *T. alpinum*. He also speaks of the great variation in corniculi in many species. FERNALD (7) found very complete intergrades between *T. vulgare* and *T. palustre* in bracts, as well as other characters. STORK reports that uniform culture conditions produce great uniformity in seedlings from parents with widely different bract characters.

FLOWERS.—HANDEL-MAZETTI uses approximate flower number as a specific criterion, and states that flower color is undoubtedly a trustworthy character, although useless in dealing with herbarium

material. The presence or absence of pollen, used by several Scandinavian authors as a specific character, is considered by the authority just quoted to be highly variable within the species, unless the observations of other men were erroneous.

ACHENES.—These are generally regarded as affording the most critical taxonomic characters, that is, in size, form, color, beak length, pappus color, ribbing, and tubercles. Actually size is no more exempt from the laws of fluctuation in *Taraxacum* than in any plant, while form is subject to considerable modifications by pressure during development. HANDEL-MAZETTI, however, states that uniform culture conditions have less effect upon achene form than upon leaf and bract characters. Colors vary from dark brown to clear green in *T. officinale* according to SCHORBATOW, who states that the two extremes are fixed in inheritance, but whether he includes *T. laevigatum* under the other species is not clear. In STORK's cultures, chosen from parents varying as widely as possible in achene as in other characters, the progeny were either red or gray fruited. Color does not develop until the outer cells die, and in red fruits is due to homogentisic acid which is absent in gray ones (10). Freezing may prevent its appearance in *T. laevigatum* (17). Beak length is notoriously interfered with by injury, whether by freezing or mowing. Pappus color is said by HANDEL-MAZETTI to be due to diffraction phenomena and not pigment. The small species group characterized by definite pappus color is therefore likely to be a distinct one. Ribbing is due to the number of stereome bundles beneath the epidermis.

Summarizing, it is seen that while bracts and achenes are conceded to afford the critical characters, the leaves are actually given great weight in spite of their variability and the uncertainty concerning its nature. There is also not a little evidence for bract variability. Pappus color seems dependable, and achene color ought to be generally so, barring environmental extremes.

Observations

METHOD.—Several years of desultory observation in connection with other phases of this work having failed to throw the necessary light upon the problem of leaf variation, it seemed best to conduct

thorough studies of entire plants excavated from various habitats. After some fifty plants had thus been secured and studied, several hundred additional spud collections were made for confirmatory purposes. Subsequently all conclusions were tested rigorously by field observations extending over a period of fifteen months. By comparison of root development, color and texture of cortical rind, number and nature of withered petiole zones, and general condition of rosette, it was found that the age of a given plant could be told with considerable accuracy. With this technique as a basis, attention was centered upon the development of life history details and leaf form changes.

LIFE HISTORY.—This procedure revealed an intimate connection between leaf variability and life history. The first consideration is that strict accuracy forbids speaking of *Taraxacum* as a perennial plant without qualification. As stated by STORK, *Taraxacum* ordinarily does not bloom the first year. Blossoming occurs freely in both species throughout the second year. At the end of the period of most active flowering (autumn of second year or spring of third) the vigorous production of flower buds forces apart the inner leaves of the original rosette with their axillary growing points. From such growing points arise numerous secondary rosettes. As a rule several of these persist, functioning essentially as new individuals, in spite of their common root connection. Throughout the length of the root each secondary rosette has its own strand of vascular tissue. The individuality of the parent rosette can only be maintained by the cortical tissues, and these rather generally become cleft by fission and cork ingrowth. Observation indicates that such cleavage is hastened by conditions favoring rapid growth. Cleavage tends to become complete throughout the root length.

LEAF FORM.—The relations between this life history and leaf form is intimate and direct. The first leaves of a seedling (juvenile leaves) tend to be entire and smooth (fig. 1), later becoming more dissected and generally more hairy (fig. 2). In *T. laevigatum* this dissection in general reaches a higher degree than in *T. vulgare*, although the latter species, under conditions favoring luxuriant growth and numerous leaves, finally may attain an extreme degree

of dissection. When multicipital branching occurs, the new secondary rosettes consist of leaves of juvenile form, that is, tending to be smooth and entire (fig. 3). Each daughter rosette which persists then repeats the history of the parent rosette with respect to leaf form, as well as with respect to flowering habits and eventual

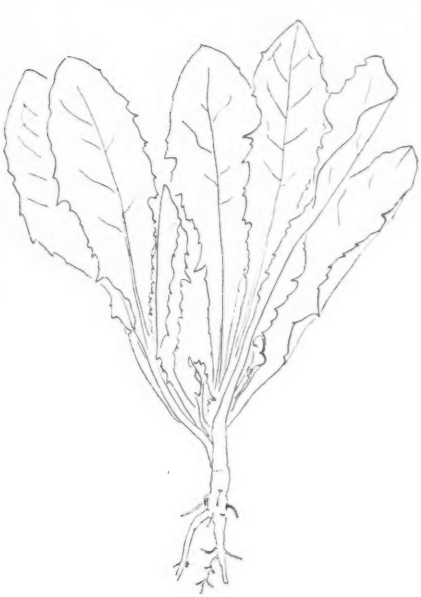

FIG. 1

FIG. 2

FIGS. 1, 2.—Fig. 1, young seedling showing relatively entire leaf form and unbranched crown; fig. 2, seedling at end of flowering period showing highly dissected leaf form, scars of juvenile leaves of first year, and beginnings of root fission.

rejuvenation (fig. 4). Certain modifying factors must be considered. For example, the supply of reserve food in rejuvenating roots results in rosettes that are often unusually vigorous and decidedly different in appearance from seedlings of the same degree of leaf dissection. Again, it not infrequently happens that secondary rosettes on the same root are of different ages, and hence different leaf form (fig. 4). This is bound to confuse an observer who does not excavate the plant and inspect it carefully.

In the next place, *Taraxacum* fruits are produced throughout the growing season and germinate readily. Very early spring seedlings may be ready to bloom before frost, and then resume blooming the following spring, equipped with highly dissected leaves. Later seedlings will not bloom until the following spring,

FIG. 3 FIG. 4

FIGS. 3, 4.—Fig. 3, plant during first season following rejuvenation, showing juvenile leaf form on each secondary rosette; degree of root fission rather unusual; fig. 4, rejuvenation of buried crown, showing formation of vertical rhizomes (note leaf scars), which secondary thickening will transform into roots; note presence of rosettes of second year (leaves highly dissected) and of first year (leaves entire).

beginning with somewhat less dissected leaves. Fall seedlings frequently seem to start blooming the next spring with almost entire leaves. In other words, the winter rest period permits many young plants to bloom which would otherwise require a greater degree of maturity or senescence.

The same relations hold true of rejuvenated plants. Secondary rosettes which have started early begin blooming the following

spring with very much segmented leaves. Those started late in the year begin to bloom the next spring with nearly entire leaves. It is not inconceivable that *T. palustre* consists of vigorous secondary rosettes of *T. vulgare* which have rejuvenated in autumn, or for some other reason flowered in more juvenile condition than usual. If occasional pure stands of such a type are to be found, it may even be suspected that ecological conditions there favor fall germination and establishment of *Taraxacum* and fall rejuvenation as a consequence. More or less entire-leaved forms, whether regarded as distinct species, varieties, or ecological forms of *T. vulgare*, are generally arctic, alpine, or temperate hydrophytic. None of these habitats favors very early spring germination or long growing season before blooming the second year.

Another source of modification comes during good growing weather in the case of plants that have completed their flowering cycle. Rejuvenation by multicipital branching occurs before the last flower scapes are gone, giving a combination of juvenile leaves with the scapes which characterize senescence. The senescent leaves, present before rejuvenation, very rapidly die and decay. This circumstance, that early leaves die as new ones are produced, is an important one. The plant thus rapidly loosens the bond connecting it with the earlier condition, resulting in an isolation of pseudotypes which are really transient phases.

Field observations have successfully applied WIESNER'S finding of the effect of moist and dry atmosphere, while experiments have verified the truth of it. The effect of a xerophytic habitat is not to increase the amount of dissection, but to shorten leaves at all stages of senescence. Juvenile leaves become nearly orbicular, whereas they may be almost spatulate in a habitat with low transpiration. Senescent leaves in a xerophytic habitat are so shortened that lobes and incisions become sharply triangular. Senescent leaves in a non-xerophytic habitat are much more graceful and very different in appearance.

ACHENES.—Aside from the failure of red pigment to develop in injured fruits of *T. laevigatum*, achene color seems to be rather a fundamental character, varying in degree but not in kind. Homogentisic acid is a highly specific substance derived from tyrosin, and neither was found in non-red fruits, according to HANDEL-

MAZETTI, already quoted. As to details of achene form, it is possible to find in a field of *T. vulgare* and *T. laevigatum* achenes varying from nearly smooth to almost shaggy. As a rule the form seems consistent in the individual plant.

FLOWERS.—Color is markedly influenced by pigmentation of styles as well as of petals, and by presence or absence of ripe pollen. That flower number per head may not always be relied upon as a criterion becomes evident from field studies. Depauperate plants whose species is unquestionable may produce a surprisingly small number, as few as fifty.

POLLEN.—In the spring of 1921 at Lincoln, Nebraska, pollenless plants, both red and gray fruited, were found, the former in abundance. Microscopic examination showed that pollen development had been arrested before the grains had separated. Certain interesting correlations were noted in the red fruited pollenless forms. The leaves are invariably dissected less than the maximum for *T. laevigatum*, and the inner bracts are twelve or thirteen in number, containing in all eighteen to twenty-two corniculi on their greenish tips. It was at first believed that this represents a distinct genetic type, and such indeed may be the case. Search revealed a number of transitional forms, however, with scant pollen, fifteen to eighteen reddish bracts, and leaves considerably dissected. *T. laevigatum* itself has copious pollen, eighteen to twenty red tipped bracts each bearing a corniculus, and leaves heavily dissected. In one case a combination of the two extremes was obtained on different rosettes of the same old root. Quantitative studies, quoted by the courtesy of Mr. H. PEGLER, show that the degree of leaf dissection in the pollenless forms increases as one passes from peripheral to central leaves, and lies exactly between the increasing dissection of a young seedling of *T. laevigatum* and the fluctuating dissection of a typical adult of the same species. It is not unlikely, therefore, that this is even a more interesting case of isolation of pseudotype than is the *T. palustre* form of *T. vulgare*.

BRACTS.—Aside from the case just described, bracts of both species have been found to vary notably in the degree of development of the corniculi, in number between twelve and twenty-two, and in color.

REGENERATION.—Mere removal of older competing leaves does not alter the degree of senescent dissection of those subsequently produced. Removal of all leaf incepts, down to undifferentiated meristem, results in production of juvenile leaves. The rhizomes produced by etiolation produce juvenile leaves when cut and placed in a moist chamber; in fact, after secondary thickening begins, pressure crushes the pith, and all rhizomes become essentially roots. Study of developing leaves shows that the juvenile leaves are produced by a disproportionate development of tip segment at the expense of the rest, while dissected leaves result from a more or less uniform development of all segments.

Quantitative studies

METHOD.—More precise analysis of the rôle of senescence as a cause of leaf dissection being desired, quantitative verification of these observations was obtained from studies of plants growing under widely different natural conditions. Prints of each successive leaf in each rosette studied were outlined by bounding polygons, and area of both leaf and polygon taken by means of a planimeter. The real area of each leaf was then divided into the difference between real and ideal (polygon) area. This, it will be seen, gives a percentage expression for the degree of dissection of each leaf.

It was finally deemed necessary, in order properly to delimit the problem, to investigate some of the correlations which more obviously suggested themselves. On the whole, these center about various phases of conductive efficiency of the xylem. Root cross-sections at various levels were studied to determine whether any correlation could be noted between cross-section areas and relative age of xylem tubes. Next the tube diameters were carefully measured at the base of successive leaf petioles in a number of rosettes. These measurements were made with an eyepiece micrometer graduated to intervals of approximately 3.33 μ. Since water conducting efficiency of a given cross-section of capillary tube is a function of the fourth power of its radius (**18**), the total capacity of each leaf was obtained by getting the sum, $(\text{diameter}/2)^4$, of all its xylem tubes. Mean capacity represents this figure divided by the number of tubes in a given leaf.

The ratio of total capacity to leaf area was also obtained in an effort to see whether it might be correlated with degree of dis-

section. Leaf area being given in terms of square millimeters, and capacity figured in terms of fourth powers of micromillimeters, the latter have been multiplied by 10^{-12} to get both sets in terms of a common unit. For the sake of compactness these figures are multiplied by 10^8 before tabulation, as noted in tables. The foregoing data will be found listed in tables I–VA and plotted in figs. 5 and 6. Here are also included counts of the number of vein islets per unit area of leaf, taken at mid-distance between margin and midrib and averaged from several counts in each case.

TABLE I

DIAMETER FREQUENCIES OF XYLEM TUBES FOR SUCCESSIVE LEAVES OF SEEDLING PLANT *SA;* EACH UNIT REPRESENTS 3.3 μ

Leaf no.	Diameters						
	1.0	1.5	2.0	2.5	3.0	3.5	4.0
1	1	2	3	7	11	2	1
2	3	9	12	9	7	2	2
3	15	6	6	3	2	.....	.....
4	2	4	12	5	3	5	7
5	1	4	16	7	5	.....	.....

TABLE I A

OTHER DATA FOR SUCCESSIVE LEAVES OF SEEDLING PLANT *SA*

	Leaf nos.				
	1	2	3	4	5
Leaf area	.....	250	125	150	100
Total xylem capacity $\times 10^8$	1.37	1.52	0.32	2.47	0.73
Mean xylem capacity $\times 10^8$	0.0510	0.0346	0.0101	0.0052	0.0222
Total capacity $\times 10^8$ / Leaf area	.....	0.0061	0.0025	0.0165	0.0073

TABLE II

DIAMETER FREQUENCIES OF XYLEM TUBES FOR SUCCESSIVE LEAVES OF SEEDLING PLANT *SB;* EACH UNIT REPRESENTS 3.3 μ

Leaf no.	Diameters															
	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5
1	.....	.....	3	5	9	7	7	2	5	6	5	12	4	6	.....	1
2	.....	1	6	5	16	10	9	8	11	5	2	1	.....	.....	.....	.....
3	.....	1	8	12	12	11	11	4	7	2	3	2	.....	.....	.....	.....
4	1	5	18	25	34	15	7	11	12	1	1	.....	.....	.....	.....	.....
5	2	9	19	12	15	24	12	2	.....	.....	.....	.....	.....	.....	.....	.....
6	3	10	7	9	17	12	7	2	.....	.....	.....	.....	.....	.....	.....	.....
7	.....	5	6	6	14	10	10	4	4	1	.....	.....	.....	.....	.....	.....
8	.....	6	5	6	6	10	11	2	.....	.....	.....	.....	.....	.....	.....	.....

TABLE II A

OTHER DATA FOR SUCCESSIVE LEAVES OF SEEDLING PLANT *SB*

	Leaf nos.							
	1	2	3	4	5	6	7	8
Leaf area	1335	896	1232	1575	1058	806	.....	.....
Leaf dissection	0.01	0.01	0.02	0.08	0.12	.....	.....	.....
Total xylem capacity $\times 10^4$	57.24	18.71	16.36	17.10	7.33	4.86	8.14	4.62
Mean xylem capacity $\times 10^4$	0.7950	0.2529	0.2241	0.1315	0.0772	0.0726	0.1358	0.1005
Total capacity $\times 10^8$	0.0428	0.0208	0.0132	0.0108	0.0069	0.0060	.....	.....
Leaf area / Vein islets per unit leaf area	13	12	12	12	10	9	.....	.....

TABLE III

DIAMETER FREQUENCIES OF XYLEM TUBES FOR SUCCESSIVE LEAVES OF SEEDLING PLANT *SC;* EACH UNIT REPRESENTS 3.3 μ

Leaf no.	Diameters												
	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0
1	.....	3	10	5	15	7	16	2	15	2	5	1	.....
2	.....	5	17	14	39	21	34	10	28	8	13	4	.....
3	1	2	11	4	16	17	9	10	13	6	3	2	1
4	.....	6	4	8	24	5	20	4	17	1	2	.....	.....
5	2	3	14	11	27	16	11	6	5	.....	.....	.....	.....
6	.....	3	12	10	18	15	14	6	6	.....	.....	.....	.....
7	.....	5	11	13	16	16	20	4	10	3	2	.....	.....
8	2	10	15	10	23	20	17	6	4	1	.....	.....	.....
9	4	6	10	13	29	18	1	1	.....	.....	.....	.....	.....
10	4	9	11	16	19	6	3	.....	.....	.....	.....	.....	.....
11	4	8	11	17	15	14	5	2	.....	.....	.....	.....	.....
12	2	9	10	14	10	7	13	3	1	.....	.....	.....	.....

TABLE IV

DIAMETER FREQUENCIES OF XYLEM TUBES FOR SUCCESSIVE LEAVES OF SEEDLING PLANT *SD;* EACH UNIT REPRESENTS 3.3 μ

Leaf no.	Diameters										
	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0
5	3	12	14	9	16	4	3	.....	.....	.....	.....
6	2	10	22	17	18	6	2	.....	.....	.....	.....
7	1	11	31	9	13	5	.....	.....	.....	.....	.....
8	.....	15	17	12	22	14	10	2	.....	.....	.....
9	1	9	34	13	26	6	4	.....	.....	.....	.....
10	2	8	16	18	10	4	3	.....	.....	.....	.....
11	4	10	20	11	13	4	1	.....	.....	.....	.....
12	2	3	11	6	21	7	6	.....	.....	.....	.....
13	4	3	6	6	15	12	9	5	5	3	.....
14	.....	2	5	9	11	11	14	5	5	.....	.....
15	.....	1	6	9	16	9	11	4	7	1	1
16	.....	2	7	8	17	8	13	.....	7	.....	.....
17	1	.....	12	3	11	13	9	.....	3	.....	.....
18	1	2	10	5	10	5	8	3	.....	.....	.....

TABLE III A

OTHER DATA FOR SUCCESSIVE LEAVES OF SEEDLING PLANT *SC*

	Leaf nos.											
	1	2	3	4	5	6	7	8	9	10	11	12
Leaf area	.....	.....	2013	1581	1425	1290	1155	1387	993	.....	.....	.....
Leaf dissection	.....	.....	0.05	0.12	0.18	0.15	0.22	0.20	0.36	.....	.....	.....
Total xylem capacity $\times 10^8$	20.72	41.00	25.98	18.43	10.50	10.85	17.46	12.13	4.91	3.15	4.85	6.05
Mean xylem capacity $\times 10^8$	0.2558	0.2124	0.2734	.02025	0.1106	0.1292	0.1746	0.1123	0.0599	0.0463	0.0638	0.0876
Total capacity $\times 10^8$												
Leaf area	.....	.....	0.0129	0.0116	0.0073	0.0084	0.0151	0.0087	0.0049	.....	.....	.....
Vein islets per unit leaf area	7	7	8	8	9	11	12	.....	.....	.....	.....	.....

TABLE IV A

OTHER DATA FOR SUCCESSIVE LEAVES OF SEEDLING PLANT *SD*

	Leaf nos.													
	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Leaf area	400	270	425	787	709	535	387	554	645	967	903	580	541	309
Leaf dissection	0.04	0.11	0.07	0.09	0.15	0.18	0.23	0.30	0.31	0.43	0.42	0.64	0.54	0.72
Total xylem capacity $\times 10^8$	2.55	3.03	2.06	6.23	3.95	2.46	2.08	3.64	10.39	9.05	10.86	8.24	5.63	4.03
Mean xylem capacity $\times 10^8$	0.0418	0.0394	0.0295	0.0678	0.0424	0.0403	0.0331	0.0650	0.1522	0.1460	0.1671	0.1330	0.1083	0.0916
Total capacity $\times 10^8$														
Leaf area	0.0063	0.0112	0.0048	0.0079	0.0055	0.0046	0.0053	0.0065	0.0161	0.0093	0.0120	0.0142	0.0104	0.0130
Vein islets per unit leaf area	17	16	18	11	13	12	.....	12	9	8	9	10	9	.....

TABLE V

DIAMETER FREQUENCIES OF XYLEM TUBES FOR SUCCESSIVE LEAVES OF REJUVENATED PLANT *R*; EACH UNIT REPRESENTS 3.3 μ

Leaf no.	Diameters															
	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5
2		2	13	13	19	5	8	6	13	7	12	3	9	4	6	1
4		8	18	10	32	11	25	8	17	5	13	2	10	2	1	....
6		5	10	7	22	14	24	15	25	11	6	2	....	....	....	....
8	1	4	10	10	16	14	20	11	15	7	8	....	1	....	....	....
10		9	23	14	13	12	17	15	10	5	3	....	....	....	....	....
12		3	6	9	11	5	12	3	10	7	6	....	3	....	....	....
14		....	7	7	11	5	9	8	10	3	8	3	3	....	....	....
16		....	6	4	11	1	10	3	6	5	7	3	....	....	....	....

For comparative purposes, distortion figures have been worked out so far as trustworthy available data permit. These are based upon changes produced by senescence (original), depauperation (**2**), and moisture (**20**). It is to be regretted that the only established facts with regard to light are its axiomatic effects upon leaf position and the effect of darkness in stimulating the production of internodes. The method used in working out these figures should be apparent from inspection, and can be found adequately discussed by THOMPSON (**19**).

In addition to these methods, microchemical studies were made throughout the summer of 1921 on tissues of *T. vulgare* plants in all stages of senescence and rejuvenescence.

RESULTS.—In general it will be noted that the percentage of dissection in various plants of *T. vulgare* tends to rise at a uniform rate. Studies of second year flowering plants indicate that after a value of 0.5 is attained, the degree of dissection fluctuates about that as an approximate mean until late in the flowering period. Then, as previously noted, if many leaves have been produced, the curve may rise to a higher value.

With respect to *T. laevigatum*, fewer determinations are at hand and none are listed. All that have been made indicate that the rate of increase of dissection is not so rapid, but continues until a value of about 0.8 is reached, fluctuating about this value during the adult period proper.

That the increase in degree of dissection is not merely a veiled expression of progressive decrease in leaf area is evident from fig. 5.

TABLE VA

OTHER DATA FOR SUCCESSIVE LEAVES OF REJUVENATED PLANT *R*

	Leaf nos.															
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Leaf area	1806	.....	.....	1584	1741	1322	.....	2735	2138	2432	2025	1896	1064	739	870
Leaf dissection	0.13	.....	.....	0.25	0.30	0.41	.....	0.41	0.40	0.49	0.50	0.44	0.51	0.49	0.57
Total xylem capacity $\times 10^8$	70.86	.....	64.70	.....	41.02	.....	32.27	.....	25.10	.....	28.80	.....	30.21	.....	21.31
Mean xylem capacity $\times 10^8$	0.5856	.....	0.3994	.....	0.2969	.....	0.2758	.....	0.1976	.....	0.3556	.....	0.4083	.....	0.3806
Total capacity $\times 10^8$	0.0392	.....	.....	.....	0.0235	.....	.....	.....	0.0117	.....	0.0142	.....	0.0283	.....	0.0245
Leaf area / Vein islets per unit leaf area	.....	.....	15	10	11	11	14	9	12	.....	13	.....	16	15	.....

It will be noted that absolute leaf area decreases rather uniformly in *SC*, a seedling plant grown under apparently favorable conditions. On the other hand, *SD*, a seedling that started under hard conditions (tight, dry clay), shows a gradual uniform increase. Of course these facts are established easily by familiar observation, but they are mentioned here to show the positive necessity of studies based upon field material growing under varying natural conditions. Not only here, but in connection with studies of xylem capacity, very erroneous ideas of senescent correlation might have been obtained by limiting studies to uniformly grown culture material, as a glance at the graphs will show.

Total and mean xylem duct capacity measured and computed as stated show a seeming correlation with degree of senescence in the cases of *SB* and *SC* seedlings, and somewhat less in the case of *R*, a secondary rosette. The possibility that this correlation is real, however, is quite upset by data on the depauperate seedlings *SA* and *SD*.

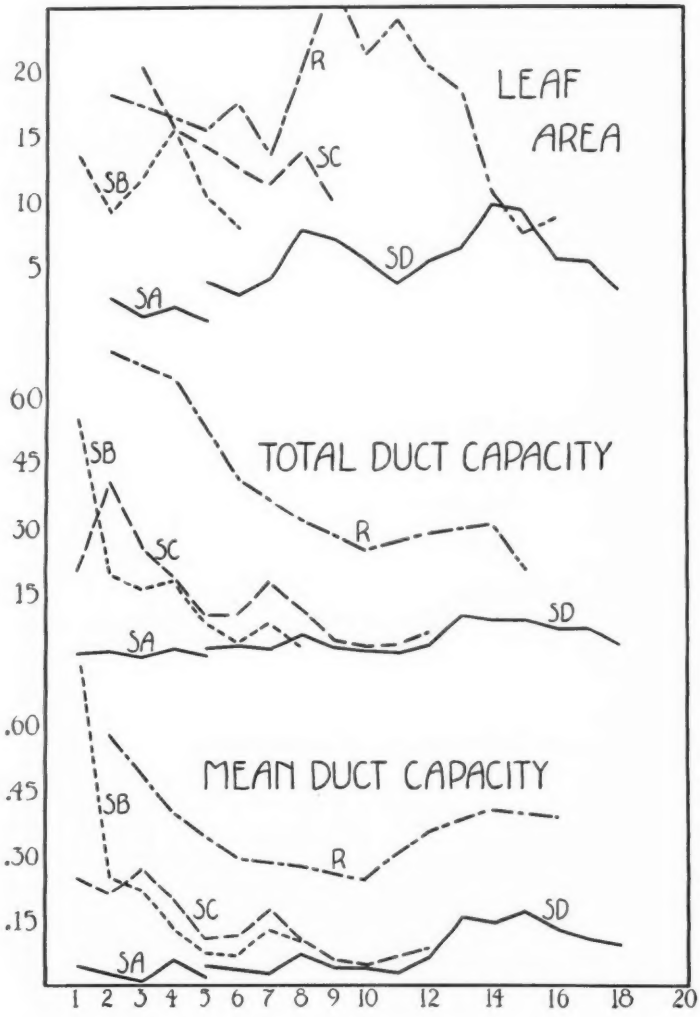

FIG. 5.—Abscissae represent successive leaves of various rosettes, ordinates the respective characters measured in each set of graphs; *S*, seedlings; *R*, rejuvenated rosette.

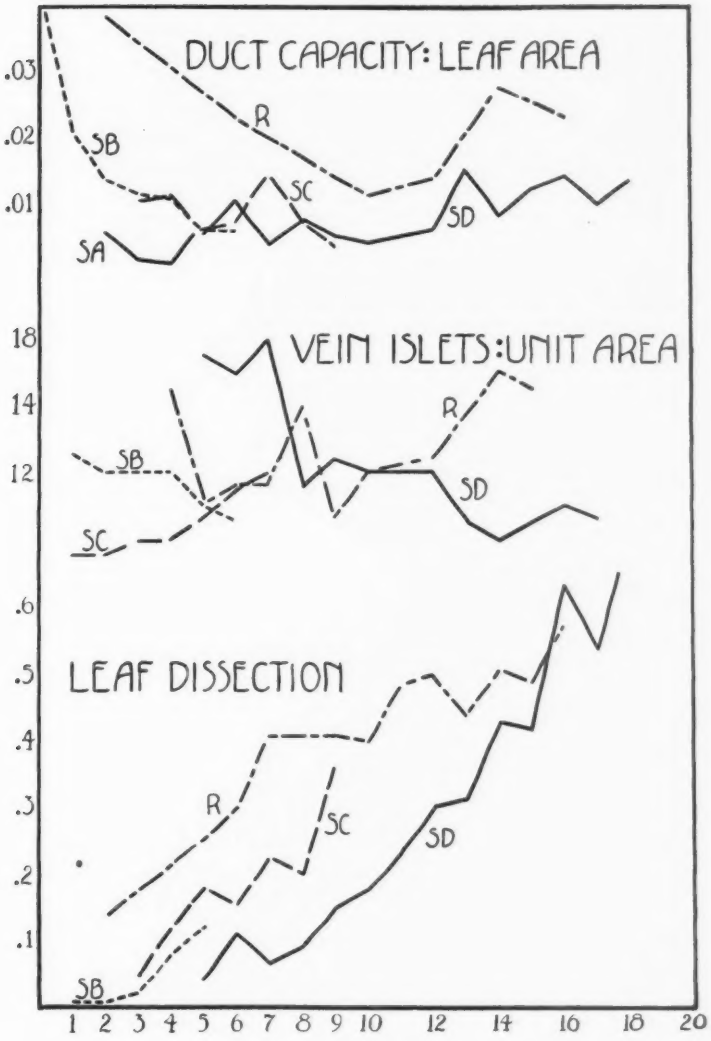

FIG. 6.—See explanation of fig. 5

Both of the latter showed steady increase in leaf dissection, although through an accident to the print of *SA* its dissection data could not be worked out. As with leaf area, therefore, total and mean duct capacity are plainly influenced by some factor other than senescence, doubtless environmental.

Essentially the same statement may be made with respect to the ratio (duct capacity / leaf area) and to BENEDICT'S (1) criterion (vein islets / unit leaf area), from which we may at least

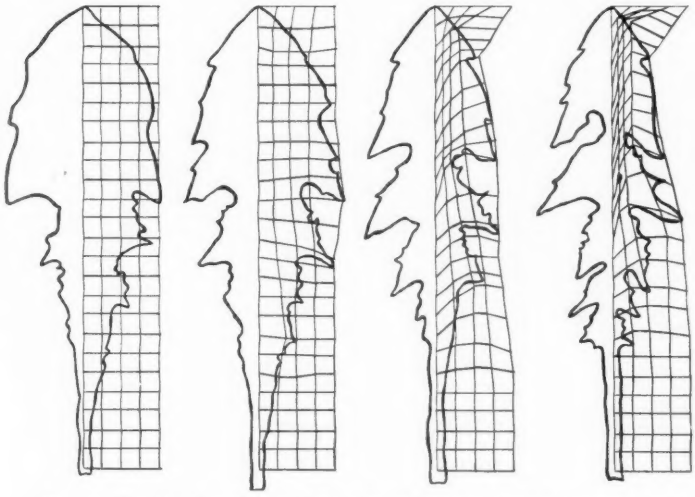

FIG. 7.—Showing, from left to right, effect of senescence on successive leaves of rosette; coordinates run through homologous points in each case.

with safety conclude that the criterion for senescence in *Vitis* certainly is no criterion in *T. vulgare*. Since the completion of the present work, ENSIGN (6) has shown a similar lack of correlation between vein islet area and age in several genera, including even *Vitis*.

Distortion figures for senescent change (fig. 7) are chiefly of value in showing that the successive sets of forms in a rosette can be homologized. They likewise show, what seems clear from inspection of ordinary leaves, that the increase in degree of dissection is the result of an increasing degree of inhibition of the tip

segment and of expression of the following segments. Fig. 8, derived from BONNIER'S (2) transplanting experiment, shows in leaves of corresponding age a rather uniform reduction of coordinates throughout, that is, more or less symmetrical reduction of leaf size. Numerous observations of the writer upon potted specimens of the same age, growing side by side but in pots of different

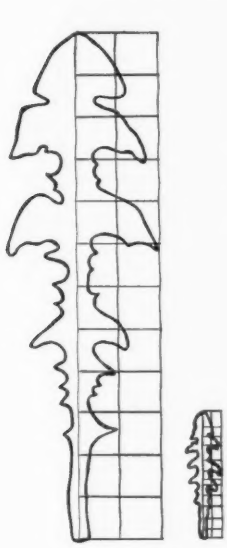

FIG. 8

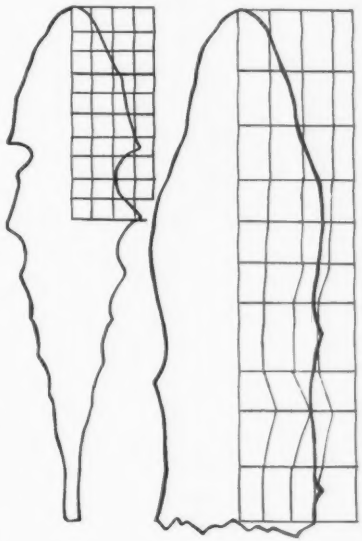

FIG. 9

FIGS. 8, 9.—Fig. 8, showing relatively uniform dwarfing brought about by alpine conditions (right) as compared with lowland (left); after BONNIER; fig. 9, showing great increase, particularly in length, produced by saturated (right) as compared with somewhat dry air (left); after WIESNER.

sizes, indicate that symmetrical dwarfing (depauperation) does occur without greatly influencing leaf form. Under such conditions the depauperate specimens produce markedly fewer leaves, and as a consequence may be ready to bloom before dissection has progressed quite so far as in normal thrifty specimens. Facts of this nature must be thoroughly understood before "alpine" forms of *Taraxacum* are pronounced distinct species, or the generalization

drawn that unfavorable conditions per se tend to produce entire leaves.

WIESNER's figures of the effect of increased moisture, while in general borne out by the writer's observations, must be accepted with reserve upon one detail. It is by no means certain that the slight degree of dissection visible in the smaller dry-air leaves can be attributed to environmental factors (fig. 9). As previously noted, WIESNER merely indicates that both sets of leaves were from the same parent plant. It frequently happens that multicipital branches of various ages occur upon the same taproot (fig. 4). Experiments show that the moist-air leaf which he figures is the typical form obtained by placing a juvenile rosette with undissected leaves beneath a belljar. Furthermore, the driest conditions under which *Taraxacum* will grow do not prevent the normal sequence of entire leaves followed by more dissected ones, although it is quite conceivable that they may affect the rate of senescence. In the last place, if a mature rosette be placed in saturated air, dissected leaves are produced until rejuvenation occurs. The distortion figures show, bearing these reservations in mind, that saturated air causes production of leaves that are larger and considerably longer than those grown in drier air.

Microchemical tests upon plants of various ages and degrees of leaf dissection have revealed a number of points of physiological interest, of which only one will be mentioned here. In all plants tested, from whatever habitat, juvenile leaf form was accompanied by high nitrate tests and little reserve carbohydrate. This is not unique; unpublished studies of ECKERSON, working with KRAUS at Wisconsin, show that leaf dissection of tomato is increased by scarcity of nitrate as compared with carbohydrate. It is moreover of interest to recall LONG's (**13**) finding, that inner leaves of *Taraxacum* rosettes are richer in photosynthate than outer.

In conclusion, it is to be noted that a rather extensive survey of published species descriptions reveals that a considerable number of them will fit variants of either *T. vulgare* or *T. laevigatum* caused by the interplay of the factors that have been described. While this statement is presented upon the writer's responsibility, without detailed data, it may readily be verified in one case by an inspection

of the figure and description of *Leontodon latilobum* given in BRITTON and BROWN'S *Illustrated flora*, 2d ed. It is clearly a juvenile rosette and hence not a valid type for comparison. Possibly it is flowering in the juvenile condition because of an autumnal start followed by a winter rest, as previously described. It certainly may be a legitimate distinct species, and so may a great many others, but it is not too much to suggest that taraxacologists have been ignoring grave sources of error, and to insist that future diagnoses be placed upon a satisfactory physiological basis.

Summary

1. Senescent and rejuvenescent change in leaf form is a prime factor in producing variations in *Taraxacum vulgare* and *T. laevigatum*.

2. Senescence produces a steadily increasing degree of dissection, and frequently of hairiness; rejuvenescence restores the unsegmented juvenile seedling leaf form.

3. These changes are independent of changes in (*a*) absolute leaf area, (*b*) total xylem duct capacity in successive leaves, (*c*) mean xylem duct capacity in successive leaves, (*d*) ratio of total capacity to leaf area, and (*e*) number of vein islets per unit area of leaf.

4. Senescence, however, is accompanied by a marked increase in carbohydrate-nitrogen ratio and rejuvenescence by its abrupt decrease.

5. Environmental factors are of secondary importance in so far as studied. Moist atmosphere causes elongation of leaves. Time of seeding may govern time of flowering and rejuvenation; this in turn may affect degree of dissection in plants at flowering time.

6. Pure stands of distinctive variants in certain cases may be explained by environmental control of seed germination time.

7. The majority of so-called specific characters in *Taraxacum* are subject to extreme fluctuation.

8. These fluctuations in other than leaf characters are in some cases due to senescent change, in others to environmental factors, but mostly to causes not known.

9. Such fluctuations, together with senescent and ecological changes in leaf form, are potent enough when working upon the

two common species to produce phenotypes duplicating many so-called species.

10. Many such species may be valid, but so far the physiological evidence has not been obtained.

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ANATOMY OF EQUISETUM GIGANTEUM

ISABEL M. P. BROWNE

(WITH SEVEN FIGURES)

I. Material

While studying the anatomy of the cone of *Equisetum giganteum* serial preparations were made of some of the upper nodes of the fertile branches. These branches are small and usually possess eleven ribs and bundles. They were collected in Chili by Professor R. C. MCLEAN, who most kindly handed them over to me. Serial transverse sections have also been prepared from the upper part of a large young main stem of *E. giganteum* from the West Indies, for which I am indebted to Professor F. W. OLIVER. This series of sections extended from a level distinctly below one node to a point near the upper limit of the next node. The complete internode was about 1 cm. in length, and would doubtless have elongated much more. This stem had thirty-two bundles and ribs.

So far as I am aware, all accounts of the anatomy of *E. giganteum* since MILDE's (11) in 1867, are based upon a short description by GWYNNE-VAUGHAN (7) that appeared in 1901. As my observations differ in some points from his, and in others supplement and confirm the details given by him, it seems advisable to publish a short account of the specimens studied.

II. Node of young main stem

Taking first the large young vegetative stem, the internode possesses a wide central cavity, about 6 mm. in diameter, the total diameter of the stem being about 7.75 mm. The bundles are oval in shape, with the longer axis directed radially, and each is surrounded by a separate endodermis.[1] The vallecular canals are about the size of the bundles and of much the same shape as these. Under each rib of the stem is a tooth of sclerenchymatous fibers,

[1] In none of the internodes examined was any trace observed of the common outer sheath of the bundles figured by MILDE (*pl. 21, fig. 4*).

projecting inward to within one to four cells of the endodermis surrounding the bundles.

The carinal canals are large, especially considering the youth of the specimen, and occupy about one-third of the bundle. The remains of one or two tracheids may adhere to the edges of the carinal canal, but all trace of the protoxylem has frequently disappeared over long stretches. The metaxylem forms two lateral, nearly parallel bands that converge slightly toward the periphery of the bundle. Usually each band consists of a single row of tracheids, although locally there are often two tracheids lying side by side. In any case the band of metaxylem is markedly narrower toward the periphery of the bundle, because the tracheids here are always much smaller. The tracheids, of which each band contains from seven to fifteen, usually about twelve, increase steadily in size toward the interior of the bundle. This "internodal" condition of the bundle, which in essentials is that characteristic of the whole genus, is shown diagrammatically in fig. 1, stage 1.

The node was slightly oblique, so that a section apparently nearly accurately transverse of the individual strands showed many different stages of nodal development. In the diagrammatic figures advantage has been taken of the opportunity to show two or three neighboring bundles in successive stages.

The increase in the amount of metaxylem first becomes apparent about 1200–1600 μ below the level of the actual departure of a trace. The additional tracheids are situated between the inner ends of the bands of metaxylem. There is no regularity in their order of development. Sometimes the first to lignify are those in contact with the tracheids of the lateral bands, but at other times the first additional tracheids to be formed lie in the middle of the parenchyma between the bands (fig. 1, stage 2). These tracheids are much smaller than the relatively large xylem elements situated near the inner ends of the lateral bands on which they abut. Generally the crossbar which is thus formed is at first only one tracheid deep, but it may attain locally a depth of two or three tracheids, even before the bar is complete. *Pari passu* with its formation, other relatively large tracheids develop in contact with the inner

ends and flanks of the lateral bands of metaxylem. This phase is represented in fig. 1, stage 3. During these and the two subsequent stages figured, certain partially torn elements of protoxylem may be found adhering to the carinal canal. Their presence is

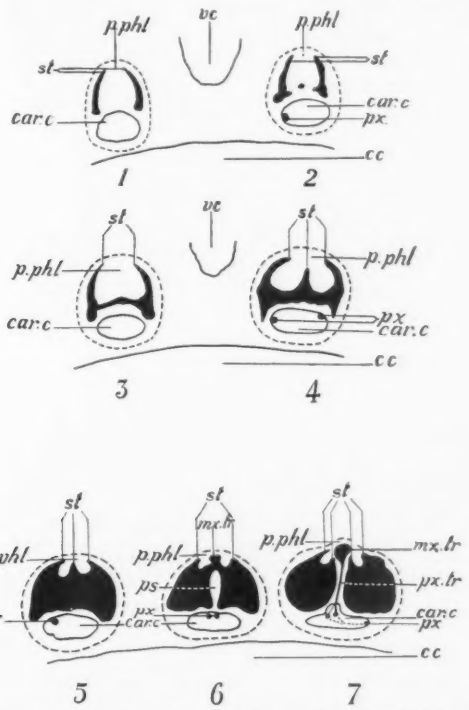

FIG. 1.—Stages 1–7, showing changes undergone by individual bundles in lower part of nodal region (xylem shown as black and endodermis as broken line): *cc*, central cavity of axis; *vc*, vallecular canal; *car.c*, carinal canal; *px*, protoxylem; *st*, small tracheids of metaxylem; *p.phl*, protophloem; *px.tr*, protoxylem of trace; *mx.tr*, metaxylem of trace; *ps*, parenchymatous sheath surrounding departing protoxylem of trace; ×120.

very inconstant; they may be absent from many consecutive sections, nor is their frequency correlated with the increase in xylem which continues as the node is approached.

As we pass upward, the tracheids of the crossbar increase in number and size, especially in its median region, where the increase

leads to the formation of an outwardly projecting tooth (fig. 1, stage 4). The tracheids at the outer edge of the tooth are very small, and have exactly the same appearance as those at the outer edge of the parallel bands of metaxylem (*st* of the figures). Their thickening appears to be a fine reticulum. The more internal elements of the metaxylem, both those of the crossbar, which becomes radially deeper, and those at the thickened bases of the former internodal lateral bands, assume more and more the appearance of typical nodal tracheids of *Equisetum;* some of them are already much widened radially. The bundles increase in width, but are still separated by intervals wider than themselves. The carinal canals are still large, but become narrower radially. The median tooth of metaxylem eventually projects nearly as far as the ends of the lateral bands and the concavities between it, and then becomes much shallower, owing to the great increase in number of nodal tracheids. This is the phase shown in fig. 1, stage 5. The small concavities in the xylem on each side of the median tooth seem to be occupied chiefly by metaxphloem.

Soon after this stage has been reached, the smaller outer tracheids of the median tooth begin to project more and more, and the tooth becomes less acute in outline. At the same time two to four rows of tracheids, lying internally to these small projecting tracheids, are replaced by parenchymatous cells. In this way the inner part of the bundle is divided by a narrow parenchymatous gully, continuous with the two or three layers of parenchyma that separate the carinal canal from the nodal tracheids. The carinal canal is now markedly narrower radially, and usually contains at its outer edge, opposite the parenchymatous gully, the remains of two or three partially disorganized tracheids. This condition is represented diagrammatically in fig. 1, stage 6. Almost immediately after the formation of the parenchymatous gully a few of the partially disorganized tracheids of the protoxylem may be seen to bend outward from the carinal canal, which here bulges a little outward. These tracheids now, no longer disorganized, run through the parenchymatous gully and fuse with the small oval mass of tracheids that forms the upward continuation of the small tracheids at the apex of the median tooth of metaxylem. These latter

elements, constituting the metaxylem of the trace, are more numerous than the protoxylem elements that pass out into the leaf. The metaxylem of the trace detaches itself from the nodal tracheids of the bundle before the phloem of the trace is set free from that of the axis. The endodermis of the bundle is beginning to bulge out somewhat opposite the trace that is preparing to depart. During its passage through the bundle (fig. 1, stage 7) the protoxylem of the trace is very clearly distinguishable under the microscope from the metaxylem, because, in a transverse section of the axis, the protoxylem running out from the carinal canal is cut almost longitudinally, while the metaxylem, some of the elements of which are not much larger, is moving so slowly and steeply upward and outward that its tracheids are cut almost transversely. When the junction of the protoxylem with the metaxylem has been effected, the tracheids of the former bend sharply upward and pursue the same steeply oblique course as the elements of the metaxylem. At this level the protoxylem is again disorganized, so that the trace contains a small protoxylem canal. This at first lies at the inner edge of the wood, but soon becomes somewhat internal in position, so that the xylem of the trace becomes mesarch almost at once. Before the trace is set free its protoxylem has assumed an approximately central position.

When the protoxylem has passed through the parenchymatous gully, two to four rows of parenchymatous cells, resembling those occurring below and on the sides of the departing protoxylem, are found above the latter. Thus the protoxylem runs through the nodal tracheids surrounded by a sort of parenchymatous sheath.[2] Immediately above the cells of this sheath nodal tracheids again form, leaving, however, a parenchymatous notch opposite the point of departure of the xylem of the trace.

Concurrently with the appearance of these tracheids the carinal canal becomes much narrower radially, and frequently contains a certain number of somewhat torn tracheids. It is usually at this stage that the nodal xylem of adjacent bundles becomes confluent. This union may take place in two ways. Where (as was

[2] Such a parenchymatous gully has also been observed at the nodes of *E. palustre* and *E. hiemale*.

the case at the points of junction of by far the greater number of bundles) the stele of a branch was inserted on the axial stele, the bundles of the latter first became united by their outer ends. Here the nodal xylem unites to form a sort of arch (fig. 2, stage 8*b*). The curve of this arch constitutes the outer and lower half of the continuous hollow central cylinder of the branch at its oblique insertion on the axial stele.[3] At a slightly higher level the more internal nodal xylem also becomes confluent, usually at a point about halfway between the periphery of the nodal xylem and its inner edge (fig. 3, stage 9). The tracheids at and near this junction

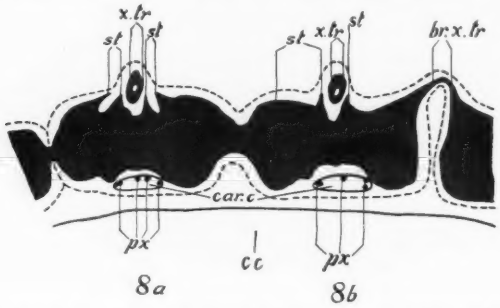

FIG. 2.—Stages 8*a* and *b*: *x.tr* xylem of trace; *br.x.tr*, xylem of branch trace; other lettering as in fig. 1; × about 120.

mark the insertion of the inner higher portion of the continuous ring of wood of the branch. At this level, however, the lower outer edge of the siphonostele is no longer visible, so that no single section shows the complete siphonostele of the branch and the continuity of its "pith" with that of the stem. Where no branch is given off, the bundles become laterally united in their middle regions by a narrow neck of xylem, as shown on both sides of the bundle in fig. 2, stage 8*a*. This neck of xylem rapidly thickens. The special endodermes lie outside the nodal tracheids, and their fusion precedes the junction of the xylem of adjacent bundles.[4] As we pass upward certain cells on the adjacent sides

[3] For a fuller description of the insertion of the vascular system of the branch on that of the stem, see PFITZER (**12**, pp. 329–330, *pl. 20, figs. 19, 20, 23*).

[4] A fuller account of the behavior of the special endodermes at the nodes will be found in PFITZER'S (**12**) description of their distribution at the nodes of *E. limosum* and *E. litorale*.

of two endodermal sheaths are replaced by single endodermal cells, common to both bundles. A little higher still these single endodermal cells are replaced by nodal tracheids, and the special endodermes by the common inner and outer endodermes typical of the vegetative nodes throughout *Equisetum*. When a branch is to be given off, the inner endodermis projects outward in a loop inside the arch of xylem representing the outer, lower insertion of the ramular siphonostele (fig. 2, stage 8*b*). In such a case the endodermal cells at the inner narrow end of the loop fuse before the junction of the nodal tracheids in this region. The endo-

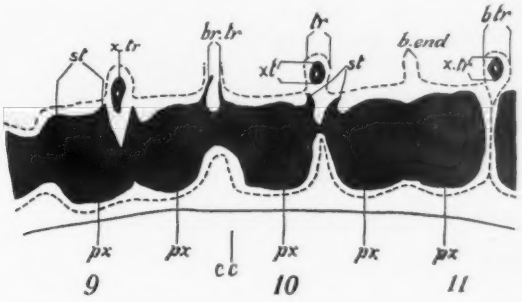

FIG. 3.—Stages 9–11; *br.x*, xylem of branch; *b.end*, endodermis of branch; other lettering as in figs. 1 and 2; × about 120.

dermis of the branch is thus in continuity with the inner endodermis of the axis.

To return to the carinal canals, these dwindle rapidly after the nodal tracheids have spread over the parenchymatous sheath, and soon disappear. As most of the medianly situated protoxylem tracheids have departed into the leaf, this region consists chiefly of parenchyma, in which are sometimes found a few tracheids that die out as we pass upward. A few of the protoxylem elements, however, forming the upward continuation of the elements at the sides of the carinal canals, may be seen persisting as two little groups on each side of the parenchymatous sinus that replaces the carinal canal. At the same time the parenchymatous depression in the outer edge of the nodal wood, opposite the departing trace, deepens, as is shown in fig. 3, stages 9 and 10. Meanwhile the inner endodermis becomes involuted into the parenchymatous

sinus at the inner edge of the xylem (stage 10). This sinus lies opposite that in the outer edge of the metaxylem, and the latter is broken in this region by the deepening of both notches; through the break inner and outer endodermes become confluent. Soon the endodermis becomes double in the region of involution, and two separate bundles are reconstituted, alternating with those of the internode below. The inner part of the endodermis of the departing trace arises as a duplication of that part of the invaginated endodermis that constitutes the bundle sheath of the new bundles at the sides of the parenchymatous depression in the outer edge of the nodal xylem. It is at this moment that the

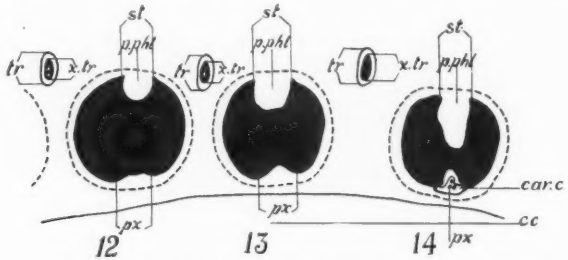

FIG. 4.—Stages 12–14: *en.tr*, endodermis of trace; other lettering as in preceding figures; × about 120.

leaf trace finally becomes free from the axial tissues (fig. 3, stage 11).

As we pass upward above the departure of the traces, the nodal xylem of the newly constituted bundles diminishes in amount, and these become more and more widely separated (fig. 4, stages 12–14). Each of them carries with it two small groups of protoxylem, situated laterally at the inner limit of the nodal xylem. Traced downward, these groups are continuous with the protoxylem of two neighboring but independent bundles of the internode below. As the nodal xylem diminishes, the two groups of protoxylem adherent to it are brought nearer to one another, each becoming farther and farther removed from its sister strand, now included in a neighboring bundle. Just before, or when the new bundles become free from one another, a slight depression appears in the outer edge of the xylem, in the median region of each new

bundle (figs. 3 and 4, stages 11, 12). This deepens rather rapidly, and another shallower parenchymatous depression appears opposite it on the inner edge of the metaxylem, between the two groups of protoxylem (fig. 4, stages 12, 13). In this inner indentation a carinal canal now forms, or, in other words, the protoxylem strands arising from different bundles of the internode below approach one another, and, partly by an increase in their number, become united into a single group (fig. 4, stage 14). By this time the metaxylem has decreased considerably in amount, and forms a deeply lobed mass, the two lobes being separated by the deepening parenchymatous sinus in the outer edge of the xylem. The lobes become less and less massive, and are soon only connected by a narrow crossbar. When this breaks, as it does a little higher up, the structure of the bundle (fig. 5, stages 15, 16) vividly recalls stages 1 and 2 of fig. 1, although the metaxylem is as yet more extensive than in these. By a decrease in the number of tracheids, however, the bundles soon assume the internodal appearance shown in fig. 1, stage 1.

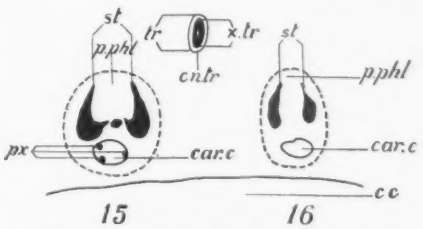

FIG. 5.—Stages 15 and 16; × about 120

As in the cone-bearing stem of *E. limosum* described by the writer (3), so at this node of *E. giganteum* an inverted cone of relatively thick-walled cells, staining deeply with Bismarck brown, hangs down from the upper limit of the node for a little distance into the internode.

III. Nodes of smaller fertile branches

The upper nodes of the cone-bearing branches of *E. giganteum*, although resembling in essentials the node of the main stem previously described, were on a much smaller scale, and showed one or two points of difference. The branches at my disposal all possessed eleven ribs and bundles, and their steles were but little over a millimeter in diameter. There is no definite diaphragm, neither is there an inverted cone of persistent tissue hanging down

from the node; but the central cavity is much narrowed in the nodal region, and the stele itself decreases somewhat in width, as is well seen in longitudinal sections. Sometimes no branches are initiated at these nodes, but in other cases one or two branches may be initiated, even at the uppermost vegetative node. As we approach the node the lateral bands of metaxylem of each bundle become united, as in the bundles of the large node already described. The bundles, at the corresponding heights, have much the appearance of those shown in fig. 1, stages 1–3, except that by the time we reach stage 3 the carinal canal is being replaced by a group of slightly disorganized tracheids. The median tooth of xylem seen in stage 4 of fig. 1 is not developed, although in some of the bundles the crossbar is slightly thicker in its median region. As in the larger axis, the crossbar is separated from the carinal canal by two or three layers of parenchyma. Some of the protoxylem elements pass out very gradually, carrying with them such of the metaxylem elements of the crossbar as lie outside them. The same parenchymatous sheath is formed for the passing out of the protoxylem. This sheath, which is relatively wide and conspicuous, is here directed obliquely upward, since the protoxylem, which lies in it, passes very slowly through the bundle. As there is here no median tooth of metaxylem, the metaxylem of the trace is more deeply situated in the bundle and nearer to the protoxylem, so that the protoxylem and metaxylem of the trace form, in most of their course through the bundle, a single, radially elongated mass of similarly oriented tracheids. This stage is shown in fig. 6, stage 1, a stage corresponding more or less with stage 7 of fig. 1. While passing through the bundle, the metaxylem of the trace remains in contact at its outer end with the nodal xylem of the

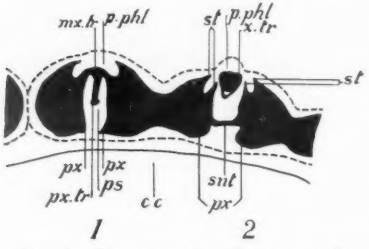

FIG. 6.—Stages 1 and 2; these stages show appearance of bundles of small cone-bearing branch of *E. giganteum* at levels of node corresponding to those shown for bundles of main axis in stages 7 and 8 of figs. 1 and 2; more highly magnified.

bundle. When the xylem of the trace detaches itself from the axial wood, it forms an isosceles triangle, sometimes containing one or two parenchymatous cells. At the inwardly directed apex of the triangle lies the protoxylem. In most cases at least, a few of the tracheids at the sides of the wide, outwardly directed base of the triangle are derived from the peripheral nodal xylem of the bundle. By the time the trace has become free and provided with a separate endodermis, its xylem has become or is becoming slightly mesarch. As the trace moves out, a bar of metaxylem, usually only one cell in depth, forms across the inner end of the parenchymatous sheath (fig. 6, stage 3). These tracheids very soon die out in passing upward. Although few in number, they seem to represent the much greater extent of median supranodal xylem of stages 8*a* and 8*b* of fig. 2.

It should be pointed out that, as in the node of the larger axis, some elements of the protoxylem, although here only a very few, persist on either side of those that depart to the trace. Each of the reconstituted bundles possesses two groups, derived respectively from the two bundles alternating with it in the internode below. Owing to the smaller size of the bundles, these two groups of protoxylem are nearer to one another than in the bundles of the main axis. They soon unite, forming with additional elements the protoxylem strands of the new internode. These groups of protoxylem traversing the node are very small and inconspicuous, and might easily be overlooked or taken for the narrow ends of nodal tracheids. It is possible that sometimes one of them may die out and not be continued in the internode above, but this could not be satisfactorily determined from the material.

IV. Branches initiated on main stem

One point in connection with the numerous branches initiated on the large young axis of *E. giganteum* deserves mention. None of these branches, the cells of which were active in process of division, had yet broken through the tissues of the leaf sheath of the parent axis. As they alternate with the teeth of this sheath, their median line coincides with the commissural furrow, or line of congenital fusion of two leaves. This furrow projects markedly

inward, causing a slight depression in the ochreola or lowest sheath of the branch. The ochreola, which is much better developed on the side away from the parent axis, possesses five teeth, forming in the lower part of the sheath five inconspicuous blunt ribs. The two which lie most externally, right and left of the slight median depression, are by far the most developed. Even in this early stage, in most cases at least, both possess a small vascular bundle containing two or three small tracheids. Cases have previously been recorded and figured in which the ochreola is penetrated by one vascular bundle (**8, 11**).

V. Young internode of main stem

The base of the leaf sheath is concrescent with the axis. At the level at which the former becomes free in the large young axis the tissues of the main stem have the appearance of being very young. The cells mostly have large nuclei and are rich in contents; no metaxylem has been differentiated, nor is the bundle sheath recognizable; most of the protoxylem still persists. The cortical cells below the ribs of the stem, which later develop as sclerenchymatous fibers, still have unthickened walls. As we pass upward in the internode the tissues gradually assume a more mature appearance. This should be expected, since it is known that the metaxylem of an internode undergoes lignification from above downward (**1**). In this lower end of a young internode, therefore, we have an anatomically incompletely differentiated portion of the axis of *E. giganteum*, the absence of which prevented GWYNNE-VAUGHAN from definitely establishing the direction of lignification of the lateral metaxylem in this species. He suspected that the direction of lignification in *Equisetum* generally was centripetal in the lateral strands of metaxylem. He held that this was indicated by the constantly smaller size of the peripheral tracheids in *E. giganteum*, the species in which the lateral metaxylem is most abundantly developed.

Near the base of the young internode, at the point at which the leaf sheath detaches itself from the axis, no metaxylem had been differentiated. As we pass upward one or two laterally situated tracheids soon make their appearance, but in most of the bundles it

is only about 1 mm. higher up that the lateral metaxylem consists of a number of tracheids more or less equivalent to the number found in a mature internodal bundle. The serial sections were 14 μ in thickness, and thirty-two bundles of a section often showed different stages of the differentiation of the laterally situated tracheids. It was possible, therefore, to examine very numerous examples of incompletely differentiated metaxylem. Some irregularities were observed, but no doubt was possible that in the very great majority of cases the small outer tracheids are the first to become lignified. Thus in this species, as GWYNNE-VAUGHAN suspected, the metaxylem develops centripetally. Not infrequently, after the lignification of two or three small elements at the periphery of the wood, the next element to be lignified is larger and much more deeply seated. Commonly, however, the lignification proceeds more or less regularly from without inward.

VI. General considerations

Conflicting statements have appeared as to whether the protoxylem of *Equisetum* persisted through the nodes or disappeared at this level. JEFFREY (**9**), in 1899, wrote that in the nodal region the vascular tissue was massive and entirely devoid of typical protoxylem elements, and in comparing the node of *Equisetum* with the description given by WILLIAMSON and SCOTT of that of a Calamite, he states that in the recent genus the protoxylem comes to an end below the node, and that it is absent from the inside of the nodal wood. LUDWIGS (**10**) also appears to regard the protoxylem as disappearing at the nodes. He writes as follows:

> At the node the protoxylem passes out as a bundle into the leaf, the groups of metaxylem approach one another and, uniting with the xylem of the next internode, completely fill up the carinal canal. In the position of the latter we find a large number of vessels with reticulately thickened walls, whereas the elements of the protoxylem show annular thickenings.

More recently Miss BARRATT (**1**) has asserted that the protoxylem does not traverse the node. In 1901, however, GWYNNE-VAUGHAN described the forking of the leaf trace protoxylem of *Equisetum* at the node and the fusion of each fork with the adjacent fork of protoxylem of a neighboring bundle. In 1908 BOWER (**2**)

adopted GWYNNE-VAUGHAN'S conclusions as to the basis of his description of the course of the bundles of *Equisetum*, illustrating this course by means of a hitherto unpublished diagram constructed by the latter.[5] QUÉVA (**14**) in his very careful researches

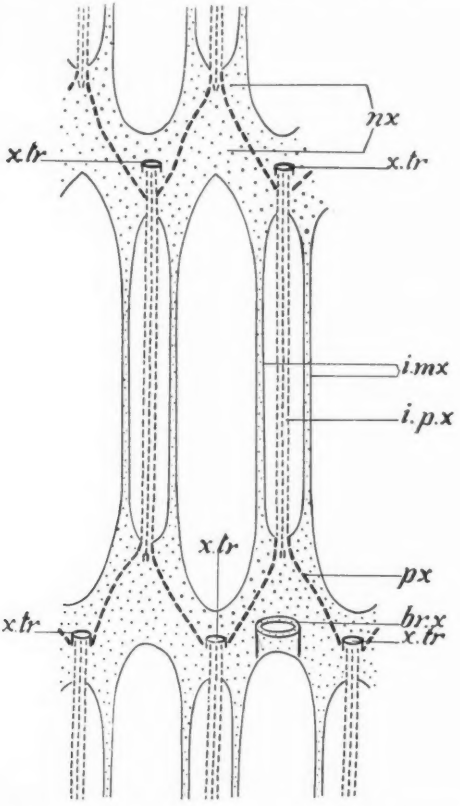

FIG. 7.—Diagram showing distribution of xylem of *E. giganteum* (protoxylem indicated by broken vertical lines, metaxylem by dotted surface): *x.tr*, xylem of trace; *br.x*, xylem of branch; *pr*, protoxylem; *i.p.x*, protoxylem of internode; *nx*, nodal xylem; *i.mx*, internodal metaxylem.

[5] This diagram is in disagreement with the comparable fig. 7 of the present paper in that in it the lateral internodal strands are made to persist through the node. As GWYNNE-VAUGHAN'S diagram was constructed only to show the course of the strands of the internodal bundle at the node, the distribution of the nodal xylem is not indicated in it.

gave no written description of the course of the protoxylem above the departure of the xylem of the trace. In describing the nodal xylem of *E. maximum*, however, he states that at the inner edge of each of the masses of nodal wood some protoxylem elements (his trachées) are always found. These axial protoxylem elements are shown before the lignification of the nodal tracheids in his figs. 16 and 17, and after the differentiation of the nodal wood in his figs. 18 and 19 (all of *E. maximum*). Moreover, his fig. 22 of *E. litorale*, in which two traces[6] may be seen, already some way out in the cortex, shows very clearly the protoxylem persisting from the bundles of the internode below. In this figure the protoxylem of each of these bundles has been divided into two groups of tracheids, and these sister groups have already diverged somewhat from one another.[7] EAMES (**6**) also regards the protoxylem as persistent, for in discussing the nodal, or as he calls it, the supranodal wood, he states: "Certainly its innermost elements are protoxylem, many radial sections show this condition clearly." Later, in summarizing the nodal structure of *Equisetum*, he states: "The carinal canal becomes discontinuous as it approaches the node. The protoxylem occupying that space enlarges, extending radially, then passes upward and forms the innermost tracheids of the supranodal wood." From these statements it would seem that EAMES holds that the protoxylem persists through the node, although hardly as distinct strands; he seems rather to regard the inner elements of nodal xylem generally as protoxylem.

The description of the nodal region of *E. giganteum* here given entirely confirms, so far as the course of the protoxylem is concerned, GWYNNE-VAUGHAN'S account. This might have been expected, as this author alone appears to have worked on the nodes of *E. giganteum*. It is, however, in agreement with QUÉVA'S less complete account of the protoxylem at the node, and in particular with his figures of *E. maximum* and *E. litorale*.

[6] Only a portion of the trace on the left is included in QUÉVA'S figure.

[7] In view of QUÉVA'S figures just mentioned, and of his allusion to the presence of protoxylem at the inner edge of the nodal wood, I cannot agree with Miss BARRATT'S statement that he had noted that the xylem of each internode develops quite independently, only linking up subsequently by the development of the nodal tracheids.

Examination of serial sections through nodes of a cone-bearing branch of *E. palustre* and of a fertile stem of *E. sylvaticum* showed that the continuity of the protoxylem strands through the node, their forkings and fusions, could very well be followed in these species. In both the course of the protoxylem at the node corresponds with that of the protoxylem in *E. giganteum*. The distinction between nodal wood and protoxylem is very clear, although the innermost nodal tracheids are relatively small. In both species the persistent protoxylem is sometimes locally separated from the inner edge of the nodal wood by a parenchymatous cell or two. In *E. sylvaticum* the persistent tracheids of protoxylem are relatively numerous, and some of the medianly situated ones may persist for a little distance above the departure of the tracheids of the trace. In a young node of a fertile stem of *E. arvense* that had not yet appeared above ground it was possible to observe the persistence of the protoxylem and indications of its forkings and fusions at the node. The phenomena, however, were not so clear.

Serial sections through a vegetative node of the cone-bearing branch of *E. debile* showed that in this species also two small groups of protoxylem, consisting of a few tracheids only, persisted after the departure of the trace. On the breaking up of the nodal xylem these two small strands entered separate but adjacent bundles. Each of the newly constituted bundles, therefore, possessed two of these small strands of protoxylem. These, however, did not always fuse to form the protoxylem strand of the internode. Frequently one, sometimes both, seemed to die out. In the latter case the protoxylem of the upper internode was unconnected (except by nodal tracheids) with that of the lower internode. In other cases a few elements of one or both branches of protoxylem linked up the protoxylem of one internode with that of the other.

In the specimens of *E. hiemale* of which I have examined serial sections, the protoxylem disappears at the nodes; in other words, the whole of it passes out into the trace. In this species the internodal bundles are relatively far apart, and the bundles of successive internodes are formed by the oblique course and fusion of adjacent halves of neighboring bundles. During the oblique course of the halves it is easy to see that all the tracheids com-

posing them are reticulately thickened. In nodes of the fertile stem of *E. maximum* I was able to trace the forking of the persistent protoxylem, the divergence of the forks, and their passage into separate though neighboring bundles. Each of the newly constituted bundles thus contained two small groups of protoxylem, but in no case could a connection between these forks and the protoxylem of the internode above be observed; they seemed always to die out.

As we are dealing in *Equisetum* with plants showing a reduced vascular system, it is probable that the dying out of part or all of the protoxylem of one internode without coming into connection with the protoxylem of the next is a derivative character, and that the course of the protoxylem described for *E. giganteum* is primitive within the genus. In this connection it may be pointed out that in the fertile stem of *E. maximum*, although the bundles are of much the same width as those of the large young axis of *E. giganteum* described in this paper, the height and the radial extent of the nodal wood of the latter, even in its young condition, were nearly twice as great as the height and depth of the nodal wood at the nodes of the fertile stems of *E. maximum* studied. Moreover, it has been shown (4) that the cone of *E. maximum* has a much reduced vascular system.

It is possible that at the nodes of the sterile stems of *E. arvense* and *E. maximum* none of the protoxylem, at least in typical cases, persists above the departure of the tracheids of the trace. This appears to be the view of JEFFREY and Miss BARRATT. On the other hand, QUÉVA's figures seem to show that sometimes at least the protoxylem persists, at any rate for some distance above the departure of the tracheids to the trace. Such protoxylem as persists at the node is small in amount and often inconspicuous, so that in many cases it may well have passed unnoticed. When, however, as in *E. hiemale*, the protoxylem disappears completely at the level of the departure of the tracheids of the trace, this would seem to be due to a further reduction along the lines exemplified at the nodes of the fertile axes of *E. debile* and *E. maximum*.

Passing from the consideration of the protoxylem to that of the metaxylem, we again meet with a conflict of evidence. In 1890

POIRAULT (13) asserted that the metaxylem developed centripetally, and eleven years later GWYNNE-VAUGHAN was led by his study of the vascular system of *E. giganteum* to adopt a similar view, although in the absence of an incompletely differentiated portion of the axis of this species he considered the centripetal development of the xylem as not established. As has been pointed out, a study of the young internode of *E. giganteum* confirms GWYNNE-VAUGHAN'S opinion, and it seems clear that in this species the direction of lignification, although subject to slight irregularities, is from without inward. On the other hand, QUÉVA in 1907 showed clearly that in *E. maximum* the lateral metaxylem of the internode was differentiated centrifugally. EAMES claimed that although there is a good deal of irregularity in the direction of its lignification, the internodal metaxylem was differentiated centrifugally in the majority of the bundles of *E. maximum*, *E. arvense*, and *E. hiemale*. This has recently been confirmed by Miss BARRATT for the first two species. Serial sections of the internodes of young cone-bearing branches of *E. arvense*, *E. limosum*, and *E. debile*, in which the lateral metaxylem was incompletely differentiated, were examined for comparison with the young internode of *E. giganteum*. In all of them the differentiation of the metaxylem, although subject to occasional irregularities, as EAMES has pointed out, was in the great majority of cases clearly centrifugal.

It seems difficult to doubt the essential homology of the characteristic lateral groups of metaxylem throughout the genus *Equisetum*. The question, therefore, arises whether the primitive order of development of the metaxylem was centripetal or centrifugal. It is undeniable that the metaxylem, both nodal and internodal, is better developed in *E. giganteum* than in any of the other species the anatomy of which has been studied. Moreover, in a genus showing an obviously reduced stelar structure the species with the largest amount of xylem would naturally seem to be the most primitive. On the other hand, *E. giganteum* is exceptional, so far as we know unique, in the centripetal development of its metaxylem. It is even possible that such centripetal development might be confined to the base of the internodes, although on general grounds and in view of the constantly much

smaller size of the peripheral tracheids this does not seem to be likely. Perhaps the strongest argument against the primitiveness of the centripetal development of the lateral metaxylem lies in the position of this tissue outside the endarch protoxylem, which makes it difficult to regard it as a vestige of the central centripetal xylem of a protostele. For the present, therefore, it seems premature to draw any definite conclusions from the exarchy of the internodal metaxylem in the axis of *E. giganteum*.

GWYNNE-VAUGHAN also stated that in *E. hiemale*, and better still in *E. giganteum*, the lateral internodal strands of xylem could be traced, after joining on to the nodal wood, as externally projecting ridges into the internode above.[8] He claimed that these lateral strands diverged while passing through the node, so that in the internode above they were situated on adjacent sides of separate bundles; that at the next node these strands again approached one another, and that in the internode above this node the strands were again included in the same bundle. In fact, according to this author, the course of the metaxylem strands at the node is exactly that described in this paper as characteristic of the protoxylem of *E. giganteum* in this region. In this species the lateral strands of metaxylem are composed of numerous elements, and if they persisted through the node they would be very conspicuous. From the serial sections of the nodes at my disposal, however, it was clear that the identity of the lateral strands was completely lost in the relatively large tracts of nodal xylem. As we approach the nodes the tracheids of the lateral strands gradually assume the appearance of typical nodal tracheids. QUÉVA has noted this gradual passing of the lateral metaxylem into the nodal wood in *E. maximum*. In this species, in which according to him the lateral metaxylem consists of tracheids with spiral or annular thickening, elements with a type of ornamentation intermediate between these and reticulate thickenings occur, he says, below the nodal wood and in continuity with the internodal metaxylem. Elements with this internodal type of thickening

[8] I regret that in a recent paper (**5**) I alluded to GWYNNE-VAUGHAN's claim of the persistence of the lateral strands "inside and over" the ring of reticulate tracheids. The passage should read "*outside* and over the ring of reticulate tracheids."

of course do not occur below the node of *E. giganteum*, since, as GWYNNE-VAUGHAN himself has shown, the internodal metaxylem, as well as the nodal xylem of this species, consists of reticulately thickened elements. Fig. 7 shows diagrammatically the distribution of the xylem at the nodes and internodes of *E. giganteum*. The spirally thickened protoxylem is there shown by broken vertical lines, while the reticulately thickened tracheids, nodal wood, and internodal lateral strands alike are shown by a dotted surface. For the sake of convenience the internodes have been drawn as much shorter than they would be in a mature specimen.

In *E. hiemale* the lateral strands are smaller than in *E. giganteum*, but it seemed clear from serial sections that they too completely lose their identity in the nodal wood. Indeed, this occurs relatively quickly, for the crossbar of the tracheids, which as we approach the node forms a bridge between the two lateral strands (fig. 1, stage 3 of *E. giganteum*), is here usually two, three, or more cells in depth, and therefore nearly as deep as the lateral strands. Thus the latter hardly project at all outward, and are early merged in an almost straight, oblong band of metaxylem lying outside and parallel to the radially narrow carinal canal. GWYNNE-VAUGHAN also claimed that in *E. maximum* no metaxylem departed from the axis to the leaf trace, although he made no statement on this point for *E. giganteum*. EAMES, however, claims that the metaxylem unquestionably takes part in the formation of the leaf trace, and figures such a case for *E. hiemale*, in which species the metaxylem is well developed. In nodes from three stems of *E. hiemale* examined the departing protoxylem carried with it metaxylem tracheids from the periphery of the bundle. At least in my specimens, however, these were less numerous than in *E. giganteum*, and died out before the trace with its endodermis was completely free from the axial bundle. In serial sections of nodes from two fertile stems of *E. maximum* and from a fertile stem of *E. sylvaticum* examined the metaxylem did not, in most of the bundles, contribute to the formation of the leaf trace, although occasionally in *E. maximum* and not infrequently in *E. sylvaticum* two or three reticulate tracheids, at the level of the departure of the trace, did bend out into the cortex, where, however, they seemed to die out.

Summary

1. The direction of differentiation of the metaxylem in the internode of *E. giganteum* is subject to slight irregularities, but is mainly centripetal. The outer elements are the smallest, and the tracheids, usually about 10–15 in number, become wider in passing inward.

2. These lateral, internodal strands of xylem join on to the nodal wood, at which level they lose their identity. There is no indication in *E. giganteum* of their persisting as strands external to the nodal wood.

3. The protoxylem is continuous through the node of *E. giganteum*. By the departure of the medianly situated tracheids to the trace the protoxylem is divided into two small groups of elements. These two groups diverge and enter neighboring but separate bundles of the internode above. Each of these small strands of protoxylem, diverging still farther from its sister strand, now situated in another bundle, fuses in the median region of the new bundle with an equivalent strand of protoxylem derived from the adjacent bundle of the internode below. The fusion is effected partly by a sudden increase in number of the protoxylem elements.

4. The nodal wood of *E. giganteum* attains a considerable height and radial depth. Wide, reticulate, typically nodal tracheids appear considerably below and persist for some distance above the departure of the traces.

5. The protoxylem elements of *E. giganteum* are situated at the interior of the xylem, and pass through the inner part of the metaxylem of the bundle in a kind of parenchymatous sheath, two to four cells in thickness. A considerable number of small metaxylem tracheids pass out into the trace, the metaxylem in the trace being usually greater in amount than the protoxylem.

6. In young branches of *E. giganteum* which had not yet broken through the leaf sheath of the parent axis, two of the ribs of the ochreola contained a small vascular bundle.

7. It is concluded that the continuity of the protoxylem of the internodes through the nodes, which, although not characteristic of all species, is not confined to *E. giganteum*, is a primitive character within the genus. The question as to whether the lateral

metaxylem of the genus was primitively centripetal, as in *E. giganteum*, or primitively centrifugal, as in the other species the detailed anatomy of which is known to us, is left open.

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OVERWINTERING OF TOMATO MOSAIC[1]

MAX W. GARDNER AND JAMES B. KENDRICK

(WITH PLATE XVII)

The annual recurrence of the mosaic disease in epiphytotic form in the canning tomato crop of Indiana has made it highly important to ascertain the mode of overwintering of the causal virus. It seemed within the realm of possibility that the virus might be perpetuated over winter in hothouse tomato crops, in tomato seed, in related perennial weed hosts, and by insects. The agency of insects in this connection has not been studied. The work of MCCLINTOCK and SMITH (**9**) on aphids as carriers of spinach blight would indicate that such insects might perpetuate other mosaic viruses, but MCCLINTOCK (**10**) has been unable to find this true for tomato mosaic. DOOLITTLE'S (**7**) work on cucumber mosaic has failed to incriminate any of the insects studied in connection with that disease. The present work has to do mainly with the second and third possibilities just mentioned.

Hothouse tomatoes as carriers

The mosaic disease has been found very commonly in hothouse tomato crops, and in the immediate neighborhood of hothouses it is possible that the disease may be carried from the late hothouse crop to the field crop plant-beds. This danger is very great in cases in which the plants for the field crop are started in hothouses or coldframes adjacent thereto. In one case noted in June 1920 at Kokomo, a severe early infestation of mosaic was present in a field, the plants for which had been grown in part of a hothouse occupied by a tomato crop. In fact, mosaic was found on many of the tomato plants left in the plant-bed. Hothouse tomatoes, however, are grown only in a relatively few localities in the state, and are usually near the towns and cities. The canning tomato crop, on the other hand, is contracted primarily among general farmers

[1] Contribution from the Botanical Department of Purdue University Agricultural Experiment Station, Lafayette, Indiana.

rather than truck gardeners, so that the fields are widely scattered through the country, and as a rule are not in the neighborhood of hothouses. Hothouses, therefore, can play only a very minor rôle as reservoirs of mosaic infection for the canning tomato crop.

Transmission with tomato seed

Miss WESTERDIJK (**12**), in her work with tomato mosaic, concluded that the disease was transmitted through the seed, but her evidence appears to be based on a field test with only ninety-six plants, and these unprotected from insects. ALLARD (**3**), in extensive tests involving about a thousand plants grown from seed from mosaic tomato plants, obtained no evidence whatever that the disease was transmitted through the seed. The same investigator (**2**) found that the related tobacco mosaic is not seed-borne.

The general occurrence of mosaic in fields used as a source of seed for the canning tomato crop of Indiana made it necessary to test thoroughly the possibility of seed carriage of the virus. A quantity of tomato seed was saved from mosaic tomato plants in the fall of 1920, in cooperation with I. C. HOFFMAN and H. D. BROWN of the department of horticulture, and was planted in a greenhouse December 2, 1920. Because of the season the plants grew rather slowly. In a careful examination made on January 20, 1921, no mosaic was found in a total of 13,573 of these plants. The crop was thinned at this date, and on February 26 no mosaic was found among the 2823 plants which remained. On February 3, 1921 seed saved from two mosaic tomato plants in 1920 was planted in soil flats in the greenhouse, and in the 135 plants present on May 9 no mosaic had appeared. In the summer of 1921 another test of tomato seed collected from mosaic plants in 1920 was made in the greenhouse and under a cloth cage in the field. The seed was planted on June 23, and on August 10 no mosaic was found in a total of 5091 plants in the greenhouse and 218 under the field cage. Thus, in a total of 19,017 plants grown from seed from mosaic tomato plants, no mosaic appeared. Similar tests in the greenhouse in 1921 with two-year-old tomato seed from mosaic plants also yielded negative results. In a total of 3927 plants grown from such seed no mosaic occurred.

The possibility of the presence of the mosaic virus dried on the exterior of the seed coat was also taken into consideration. About four ounces of tomato seed collected from mosaic plants four months previously was washed in sterile water, and eight tomato plants were inoculated by wounding the stem near the growing tip with a needle, and rubbing the wounded area with cotton soaked in this wash water. No mosaic developed in these plants. In the light of this evidence there appears to be no indication that tomato mosaic is transmitted through the seed.

Mosaic in perennial Solanaceous weeds

Historical

The susceptibility of certain perennial weeds to tobacco and tomato mosaic is highly significant in connection with the overwintering of the virus. Allard (1) transmitted mosaic from tobacco to the perennial *Solanum carolinense*, and points out the possibility of the mosaic virus persisting over winter in the rootstocks of this weed. He states, however, that he had noted only one case of mosaic occurring naturally in *S. carolinense*, but recognizes the difficulty of detecting the disease in this weed because the symptoms may be very inconspicuous. He also found the mosaic which occurs commonly on the perennial *Phytolacca decandra* to be distinct from and unrelated to the tobacco mosaic.

Nishimura (11) transmitted mosaic from tobacco to *Physalis alkekengi*. In his tests the *Physalis* plants developed no mosaic symptoms, but the juice expressed from the inoculated plants proved infectious to tobacco. This exotic species of *Physalis* is recorded as a perennial which is not hardy in the northern states. Nishimura also proved that a mosaic disease found on the perennial *Solanum aculeatissimum* in Florida by R. A. Harper was transmissible to tobacco.

Recently Crawford (6) in Iowa has reported successful cross inoculations from mosaic tomatoes to *Physalis longifolia*, a common weed of that region. He also found mosaic occurring in the field on that weed, and with the virus from the rootstocks made successful inoculations of tomato plants. He points out the probability of the mosaic virus overwintering in the rootstocks of *Physalis longifolia*. This species has not been found in Indiana.

An example of the persistence of a mosaic virus in a perennial herbaceous host is afforded by the pokeweed mosaic studied by ALLARD (**4**). The work of CARSNER (**5**) on the weed hosts of the virus of the curly-top disease of sugar beets in California has been very suggestive in connection with the problem of overwintering of mosaic viruses. He has pointed out the probability that the curly-top virus may persist over winter in *Erodium cicutarium*, a winter annual. Recent work by DOOLITTLE on the relation of *Micrampelis lobata* (**7**) and *Asclepias syriaca* (**8**) to cucurbit mosaic also has been suggestive.

PERENNIAL SOLANACEOUS WEEDS IN INDIANA[2]

The following Solanaceous perennials occur in Indiana: *Lycium halimifolium* Mill., *Solanum dulcamara* L., *S. carolinense*, *Physalis lanceolata* Michx., *P. heterophylla* Nees., *P. subglabrata* Mack. and Bush, and *P. virginiana* Mill. *S. carolinense* and the three species of *Physalis*, *P. heterophylla*, *P. subglabrata*, and *P. virginiana*, are weeds of common occurrence in and about cultivated fields. Of these, *P. subglabrata* and *P. virginiana* have been found to be by far the most abundant in the tomato regions, and most of the observations have been made upon these species. These two species are not easily differentiated, and no consistent attempt has been made in this work to separate them. The larger leaved *P. subglabrata* has appeared to be the more abundant of the two in central Indiana. Unless otherwise qualified, the term *Physalis* as used herein should be understood to refer to these two very similar species.

CROSS INOCULATION TESTS

Mosaic has been found occurring naturally in the field on *Solanum carolinense*, *Physalis heterophylla*, *P. subglabrata* (pl. XVII), and *P. virginiana*. On July 5, 1921, ten potted tomato plants in the greenhouse were inoculated by wounding the stem and rubbing the wounded area with cotton soaked in the juice from mosaic *S. carolinense* plants collected at Vincennes. By July 29 all had developed mosaic. None of the ten control plants, similarly treated except that distilled water was substituted for the juice

[2] CHARLES C. DEAM, state forester, very kindly furnished authoritative records concerning the Solanaceous flora of Indiana.

from the mosaic plants, developed the disease. On July 28, 1921, sixteen potted tomato plants in the greenhouse were similarly inoculated with the juice from mosaic *P. heterophylla* plants, and by August 18 nine had developed mosaic. Four uninoculated plants held as controls remained healthy. In a tomato field, on August 21, 1919, thirteen plants of *P. subglabrata* were inoculated with the juice from crushed leaves of mosaic tomato plants. Twelve days later eight had developed mosaic. Nearby uninoculated plants observed as controls did not develop the disease. Late in August 1919, seventeen potted tomato plants in the greenhouse were inoculated with the juice from mosaic *P. subglabrata* plants, and fourteen developed the disease; the seventeen uninoculated control plants remaining free from mosaic. On May 25, 1921, four potted tomato plants in the greenhouse were inoculated by wounding the stem with a needle and rubbing the wounded region with cotton soaked in the juice of crushed leaves of mosaic *P. subglabrata* collected at Frankfort, and fifteen days later all had developed mosaic. The two control plants, similarly treated except that distilled water was substituted for the mosaic virus, remained healthy. On July 15, 1921, forty-seven tomato seedlings grown under a cloth cage in the field were inoculated with the virus from mosaic *P. virginiana*. Ten days later twenty had developed mosaic. None of the numerous uninoculated seedlings in the cage developed the disease. The identity of this *Physalis* species was verified by PAUL C. STANDLEY of the United States National Museum. The results of these cross inoculations show that the mosaic disease found on these weeds in the field is transmissible to tomatoes.

OBSERVATIONS ON PHYSALIS MOSAIC IN 1919 AND 1920

The attention of the writers was directed to the importance of *Physalis* as a carrier of tomato mosaic in the summer of 1919. Large numbers of *P. subglabrata* occurred in an experimental field of tomatoes near Frankfort, Indiana. Mosaic became epiphytotic on the tomatoes during the latter part of the season, and also appeared on many of the *Physalis* plants, especially in a low-lying section of the field where the weeds were most abundant. In this

part of the field about 5 per cent of the *Physalis* plants showed mosaic. The reciprocal cross inoculations proved that the causal viruses were identical. *Physalis* was generally distributed in this vicinity, and a survey showed that mosaic did not occur to any extent on the plants at a distance from the tomato field. In a corn field about 40 rods distant, several hundred *Physalis* plants were examined and only two showed mosaic. Horse nettle was present in the tomato field, but showed no mosaic symptoms.

The location of a number of the mosaic *Physalis* plants in the tomato field was carefully noted. The following year this field was planted in corn and no tomatoes were grown in the neighborhood. On July 15, 1920, an inspection of the field showed the *Physalis* plants again abundant, and in the same part of the field where mosaic was noted in 1919 the disease was now conspicuous on a much higher percentage of the plants than had been observed the preceding fall. In a corn field adjacent to the west side of the experimental field, mosaic was found among the *Physalis* plants along the edge, but not over 100 feet distant from the fence. In another corn field near the east side of the experimental field, mosaic was also found on many of the *Physalis* plants. Since no tomatoes were being grown in the vicinity this season, the prevalence of mosaic on *Physalis* at this early date indicated that the disease must have persisted in the weeds over winter. The greater prevalence of the disease as compared with the preceding September may possibly be explained by the fact that many of the weeds had not shown definite mosaic symptoms in the fall, whereas the young shoots of the following spring showed conspicuous symptoms. It has been noted that mosaic symptoms on old plants in the fall may become very inconspicuous.

Overwintering of virus in rootstocks

Physalis subglabrata is perennial by means of a thick rootstock 12–18 inches below the surface of the soil, deep enough to escape harm from ordinary cultivation practices. In the fall of 1919 some of these rootstocks of mosaic plants were dug, and an unsuccessful attempt was made to carry them over winter in pots of soil. The test was repeated the next year. Late in August

1920 a number of rootstocks of mosaic *P. subglabrata* plants were dug in the Frankfort field and planted in a small plot surrounded by a wooden frame sunk in the soil in a garden at Lafayette. These rootstocks established themselves and produced shoots in the fall of 1920. The rootstocks remained alive over winter, and in the spring of 1921 sent up shoots showing mosaic. Six shoots had appeared by May 13, thirteen by May 23, and on June 3 fifteen plants were present. These mosaic *Physalis* shoots appeared well before the date that tomatoes are transplanted to the field, and all showed definite mosaic symptoms as soon as the leaves unfolded.

A number of aphids were found on these *Physalis* plants early in the season. On May 23 about twenty-five of these aphids were collected and caged on three small healthy tomato plants in the greenhouse. Fourteen days later one of these tomato plants showed mosaic. None of the six control plants developed the disease. The aphids soon disappeared from the *Physalis* plants in the field, but this test indicates that mosaic might be transmitted from *Physalis* to tomatoes by these insects.

Artificial inoculation of tomatoes with the virus obtained by crushing some of the leaves from three of these mosaic *Physalis* shoots also was successful. Ten small tomato plants were inoculated on June 24 by wounding the stem with a needle and rubbing the wounded area with cotton soaked in the *Physalis* virus. Eleven days later all had developed mosaic. Ten control tomato plants were similarly treated except that sterile water was substituted for the mosaic virus, and nine of these remained free from mosaic. These tests show that the mosaic virus persists over winter in the rootstocks of *P. subglabrata*, that the young shoots come up diseased at an earlier date than tomatoes are set out in the field, and that the disease is readily transmissible from these shoots to tomatoes.

Mosaic Physalis in fields previously in tomatoes

To determine how generally the mosaic disease was carrying over winter in the *Physalis* plants (including both *P. subglabrata* and *P. virginiana*), an examination was made in and near fields

where tomato mosaic had occurred in previous years. On May 24, 1921, an examination was made in and near the experimental field at Frankfort which had been in tomatoes in 1919, and in which mosaic was found on the *Physalis* plants in 1920. In the old tomato field, 147 out of 203 *Physalis* plants examined (or 74 per cent) showed mosaic. The disease occurred more generally distributed throughout the field, and on a much higher percentage of the plants than in 1919 and 1920. In the manner characteristic of the perennial species of *Physalis*, many of the plants occurred in clumps, and as a rule the plants in each clump were all healthy or all mosaic.

In the field west of the old tomato field, 11 out of 179, or 6 per cent of the *Physalis* plants examined in a strip about 50 feet wide along the fence showed mosaic. In the fields east of the old tomato field, 11 out of 39, or 29 per cent of the *Physalis* plants examined showed mosaic. In the field to the north, no mosaic was found on the 66 plants examined, but most of these were at a considerable distance from the tomato field. From these mosaic *Physalis* plants the disease was transmitted to tomato plants in the greenhouse, as noted in a previous paragraph. In this area, therefore, the mosaic disease persisted in *Physalis* plants two years after the tomatoes, and even became more prevalent on the weeds.

On May 23, 1921, mosaic *Physalis* plants were found in a small plot and in a field near Lafayette, in both of which tomato mosaic had occurred in 1920. On May 25, 1921, a study was made of the *Physalis* plants in a three-acre field near Indianapolis in which tomato mosaic had been especially severe in 1920. On one side of the field, 6 out of 209 *Physalis* plants examined showed mosaic, and on the other side, 67 out of 159 showed mosaic. Thus a total of 73 out of 368, or 20 per cent of the *Physalis* plants were affected with mosaic. No mosaic had been noted on the *Physalis* plants among the tomatoes in this field on September 14 of the preceding fall. In an adjacent portion of this field which had been in corn in 1920, 104 *Physalis* plants were examined and none showed mosaic.

These observations showed that the mosaic *Physalis* shoots were appearing rather generally in fields which had been in tomatoes in

previous years, well before the date when the tomato plants for the current season would be transplanted to the field. It is evident that the *Physalis* plants once infected constitute a perennial reservoir of mosaic infection, which remains a constant danger to any future crops of tomatoes (or tobacco) in the vicinity.

Further observations were made later in the season upon the prevalence of mosaic on the *Physalis* plants in fields previously planted to tomatoes. In the field near Lafayette in which tomato mosaic had occurred in 1920, 43 out of 77, or 55 per cent of the *Physalis* plants examined the third week in July showed mosaic. Many volunteer tomato plants had come up in this field, but among the 186 examined, no mosaic was found at this time, although later in the season a few developed the disease.

TABLE I

Physalis MOSAIC IN OLD TOMATO FIELDS

Field	Crop			*Physalis* plants, July 13, 1921		
	1919	1920	1921	No. examined	No. mosaic	Percentage mosaic
1	Tomatoes	Corn	Corn	79	43	54
2	Tomatoes	Oats	Clover	34	7	20
3	Tomatoes	Corn	Oats	61	16	26
4	.....	Tomatoes	Oats	27	17	63
5	.....	Tomatoes	Weeds	40	27	67
6	.....	Tomatoes	Wheat	107	55	51
7	Not tomatoes		Tomatoes	138	34	25
8	Not tomatoes		Wheat	543	4	0.7

A study of the mosaic prevalence among the *Physalis* plants was made July 13 on a large farm near Indianapolis, of which a considerable acreage was devoted to tomatoes in 1918, 1919, 1920, and 1921. The 1919 tomato crop, comprising about 100 acres, was practically 100 per cent mosaic in September. No observations were made on the 1920 crop on this farm, but it is safe to assume that mosaic was prevalent that year. Mosaic was already prevalent in the 1921 crop. The results of the survey of eight fields on this farm and the relation between previous tomato crops and *Physalis* mosaic are presented in table I. From these data it is evident how prevalent mosaic may be on *Physalis* one and two

years after tomatoes have been grown. The mosaic in field no. 7 probably was due to the tomatoes in the field at the time, since many of these also showed the disease. The scarcity of the disease in field no. 8, which had never been in tomatoes, indicates that the high incidence of mosaic in field nos. 1 to 6 was due to the previous tomato crops.

Distance mosaic may spread

Field no. 8 had never been in tomatoes before, and the nearest tomato crop, that of 1919 in field no. 1, was 400 feet distant. The few cases of *Physalis* mosaic in field no. 8 were found along the edge nearest to field no. 1, and are probably attributable to long distance transmission of mosaic from that crop. In a wheat stubble field which had never been in tomatoes, mosaic was found on *Physalis* along the edge adjacent to one of the 1919 tomato fields (field no. 3) in a strip 150–200 feet wide. No mosaic *Physalis* plants were noted at a distance of 250 feet from the edge of the field. The occurrence of mosaic *Physalis* plants along the edges of fields adjacent to the Frankfort experimental field has previously been noted. The occurrence of two mosaic *Physalis* plants 40 rods distant from this field, if attributable to spread from the tomatoes, would represent an exceptionally long distance of mosaic transport.

Surveys of numerous wheat stubble and corn fields have revealed that mosaic very rarely occurs on *Physalis* plants except in the vicinity of tomato crops, past or present. In only two instances have apparently spontaneous cases of mosaic on *Physalis* been found. One mosaic plant was found in a wheat stubble near Knightstown, and another in a corn field near Monticello. In the light of such observations it is unsafe to assume that mosaic is indigenous in these wild hosts. It seems evident, however, that once the disease is introduced by means of tomatoes, it may become enphytotic in the *Physalis* flora of the immediate vicinity.

Prevalence and correlation of Physalis and mosaic in tomato fields

To ascertain the general prevalence of *Physalis* and *Physalis* mosaic in Indiana tomato fields, and the correlation between these factors and mosaic in the tomato crop, a number of tomato fields

in six localities were examined in the summer of 1921. Of necessity much of this survey work was rather hastily performed. Included in this survey are 2 fields in Washington County visited June 29; 13 fields in Johnson County, June 30; 21 fields in Howard and Tipton Counties, July 2; 4 fields on a large farm near Indianapolis, July 13; 11 fields in Hancock County, July 20; 25 fields in Marion County, July 21; and 5 fields in Grant County, September 17. The results may be summarized as follows:

Tomato fields examined	81
Fields in which *Physalis* was found	65
Fields in which mosaic on *Physalis* was found	35
Fields in which mosaic on tomatoes was found	60
Fields in which *Physalis* and mosaic on tomatoes were found	48
Fields in which mosaic on both *Physalis* and tomatoes was found	29

The wide occurrence of *Physalis* is evidenced by its presence in 65 out of 81, or 80 per cent of the tomato fields examined. The prevalence of mosaic on *Physalis* is shown by its presence in 35 out of 65, or 54 per cent of the fields in which the weeds were noted. The prevalence of tomato mosaic is shown by its occurrence in 60 out of 81, or 74 per cent of the fields examined. Some correlation between tomato mosaic and the presence of *Physalis* is indicated by the fact that 48 out of 65, or 74 per cent of the fields containing *Physalis* showed tomato mosaic, and the fact that 48 out of 60, or 80 per cent of the fields showing tomato mosaic contained *Physalis* plants. Some degree of correlation between the occurrence of mosaic on both *Physalis* and tomatoes is indicated by the presence of mosaic on tomatoes in 29 out of 35, or 83 per cent of the fields in which *Physalis* mosaic was found, and by the presence of mosaic *Physalis* plants in 29 out of 60, or 48 per cent of the fields in which tomato mosaic was found.

Plant-bed origin of mosaic

There were convincing indications in many of the fields examined that mosaic was transported to the field with the tomato transplants. In many of the fields in Johnson and Hancock counties, originally set out with tomato transplants imported from southern states, the heavy losses in stand due to the presence of *Fusarium*

wilt in these imported transplants necessitated the use of large numbers of locally grown replants to fill the blank spaces. Mosaic was distinctly more prevalent on these locally grown replants.

An examination was made of the plant-beds in three localities which served as sources of these replants, and *Physalis* plants were found in or near these beds in all cases. No mosaic, however, was noted on these *Physalis* plants. The replants from one of these localities had been very generally diseased in every field in which they were used, and on July 20 mosaic was found very general on the tomato plants remaining in the outdoor plant-beds from which these replants had been taken. These plant-beds were grown up to weeds at this time, and thirty *Physalis* plants were found, but none showed mosaic. In fact, *Physalis* was a particularly abundant weed in this neighborhood, and was also noted in the coldframes of another grower.

The occurrence of *Physalis* plants in and about coldframes and plant-beds is considered of especial significance, because here tomato plants are grown year after year, and once mosaic gains a foothold in these weeds, all succeeding crops of tomato plants will be exposed to infection before they are transplanted to the fields. This source of infection is considered especially dangerous, because from the plant-beds the disease may be introduced into numerous fields, and because mosaic reduces the yield much more severely on plants infected when very young. It has been shown that the mosaic disease, once introduced into a locality, may persist year after year in the perennial weed relatives of the tomato. Since, under Indiana conditions, canning tomatoes are grown in rotation with other crops, and many new fields are being used each year for tomato production, the mosaic disease will undoubtedly be thus introduced into the perennial weed flora of new fields and localities each season. This will inevitably result, it would seem, in the disease becoming more and more widespread in the weed flora each year, and consequently in an alarming annual increase in the reservoir of mosaic infection for future tomato crops unless the vicious cycle is broken.

Mosaic transmission

The means by which the mosaic disease may be transmitted from *Physalis* to tomato have not been thoroughly studied, although from analogy with other mosaic diseases it has seemed safe to assume that insects are the responsible agents. Certain it is that insects are responsible for much of the spread of mosaic among tomatoes, because, by the use of cages to exclude insects, the occurrence of mosaic has been uniformly prevented. Plants thus caged remain free from mosaic in badly diseased fields.

The occurrence of aphids on mosaic *Physalis* plants early in the season, and the successful transmission of the disease to a tomato plant by these insects has been mentioned. Flea-beetles (*Epitrix cucumeris*) are abundant on *Physalis* plants throughout the season, and these insects also attack young tomato plants. A preliminary test indicates that they may carry the disease. On July 16, 1921, a number of flea-beetles collected on mosaic *Physalis* plants were placed in a large cloth cage containing young tomato plants. On August 17 six of the 338 plants in this cage showed mosaic, while no mosaic was found in the 218 control plants in a similar cage in which no flea-beetles had been placed.

Mosaic on Physalis heterophylla and Solanum carolinense

Although not as abundant as the two *Physalis* species previously discussed, *Physalis heterophylla* and *Solanum carolinense* are of common occurrence in cultivated fields in Indiana, the former usually in sandy soils. Mosaic in a conspicuous form was found in abundance on both of these species in a peach orchard near Vincennes, June 28, 1921. A clump of five mosaic *P. heterophylla* plants was found on July 27 along the edge of a field near Lafayette in which tomato mosaic occurred the previous year. Mosaic was noted on *S. carolinense* near a canning factory at Indianapolis, September 7. Successful cross inoculations of mosaic from both of these species to tomatoes have previously been described. Both species are commonly attacked by flea-beetles.

Among the eighty-one tomato fields visited in the survey, *P. heterophylla* was noted in seven fields and *S. carolinense* in thirteen

fields. In three fields, all in Marion County, mosaic was noted on *P. heterophylla* and also occurred on the tomatoes. In one of these (field no. 7) ten *P. heterophylla* plants were noted and one showed mosaic. Mosaic was noted on *S. carolinense* in only one field, a garden near Kokomo in which mosaic also occurred on *P. subglabrata* and on the tomatoes. It is evident that *P. heterophylla* and *S. carolinense* may function as reservoirs of mosaic infection. Both species are perennial by deep rootstocks and difficult to eradicate or control by cultivation.

Mosaic in annual Solanaceous weeds

ALLARD (1) transmitted mosaic from tobacco to two garden species of *Physalis* (probably annuals) and to the annual *Solanum nigrum* and *Datura stramonium*. In Indiana mosaic has frequently been noted on these weeds. Attempts to cross inoculate from *D. stramonium* to tomato and vice versa have yielded negative results. In preliminary tests mosaic has been transmitted successfully from tomato to *S. nigrum* and to *S. integrifolium* and *Lycopersicum pimpinnellifolium*. Mosaic has been noted on cultivated *Physalis pubescens*. The disease, of course, is common on tobacco, and has been transmitted to tomatoes by artificial inoculation. Mosaic has been noted on tobacco plants occurring as weeds in hothouses. While annual hosts cannot carry the mosaic disease over winter, they may serve as sources of infection during the growing season, and aid in the annual spread of the disease. Annual Solanaceous weeds are undesirable in tomato fields and plant-beds and in hothouses.

Mosaic control suggestions

The danger involved in growing plants for the field tomato crop in hothouses used for tomatoes should clearly be understood.

Tomato growers should recognize in the perennial ground cherries and horse nettle a distinct danger to their crop. Drastic measures should be taken to eradicate these weeds in the vicinity of tomato seed-beds and plant-beds. Furthermore, during the early part of the season these weeds should be destroyed or at least kept down in and around the tomato field by frequent cultivation and hand

pulling. This is especially important during the first part of the season, since early mosaic infection results in the greatest loss.

These perennial species present extreme difficulties in the way of control because of the deep rootstocks and the prompt reappearance of new shoots after the old ones are destroyed.

The annual Solanaceous weeds, such as nightshade and certain ground cherries, should be destroyed in and near tomato fields and plant-beds.

Hothouses to be used for tomatoes should be kept free from Solanaceous weeds.

Tomato plant-beds should be cleared of all weeds and remaining tomato plants as soon as no more transplants are needed.

Transplants from plant-beds in which mosaic is present should not be used.

Theoretically these weed relationships are equally important in connection with the control of mosaic in tobacco.

Summary

1. Tomato mosaic may be carried over winter in hothouse tomato crops, but this does not account for the great bulk of mosaic infection in the canning crop.

2. In a total of 22,944 tomato plants grown from seed from mosaic plants, no evidence of seed transmission of the disease was obtained.

3. The mosaic disease has been found occurring in the field on the following perennial weed relatives of the tomato in Indiana: *Physalis subglabrata*, *P. virginiana*, *P. heterophylla*, and *Solanum carolinense*. Mosaic has been transmitted to tomatoes from each of these species.

4. It has been proved that the mosaic virus persists over winter in the rootstocks of *P. subglabrata*. The young mosaic shoots appear in the spring before tomatoes are transplanted to the field. From these shoots the disease has been transmitted to tomatoes.

5. *Physalis subglabrata*, with some admixture of the very similar *P. virginiana*, is a very prevalent weed in Indiana tomato fields.

6. Examination of these weeds in fields previously in tomatoes shows that a considerable percentage of the *Physalis* plants come

up showing mosaic the next year, and likewise the second year after the tomatoes. The disease persists among these weeds year after year, and such weeds serve as a perennial reservoir of mosaic infection for future tomato crops.

7. Mosaic has not been found to any extent occurring spontaneously in *Physalis*, and is present in the weeds only in and near fields once used for tomatoes. As more and more new fields are used for tomatoes, however, the reservoir of mosaic infection in the perennial weed flora will increase each year.

8. Evidence of spread of the disease to *Physalis* plants 200 to 400 feet from tomato fields has been adduced.

9. In a field survey *Physalis* was observed in 65 out of 81 tomato fields, and mosaic was noted on *Physalis* in 35 of these fields, and on both *Physalis* and tomatoes in 29 fields. Tomato mosaic was noted in 60 fields, and in 48 of these *Physalis* was found.

10. In many fields the tomato mosaic was undoubtedly of plant-bed origin. Mosaic was found on tomatoes in plant-beds. *Physalis* is often present in and near plant-beds.

11. Aphids and flea-beetles may play a part in the transmission of mosaic between *Physalis* and tomatoes.

12. *Physalis heterophylla* was found in 7 of the 81 tomato fields examined, and in 3 fields showed mosaic.

13. *Solanum carolinense* was found in 13 of the 81 tomato fields examined, and in one field showed mosaic.

14. The eradication of perennial Solanaceous weeds in and near tomato fields, and particularly the plant-beds early in the season, is recommended as a mosaic control measure.

The writers wish to acknowledge their indebtedness to Professor H. S. JACKSON for helpful suggestions and criticism.

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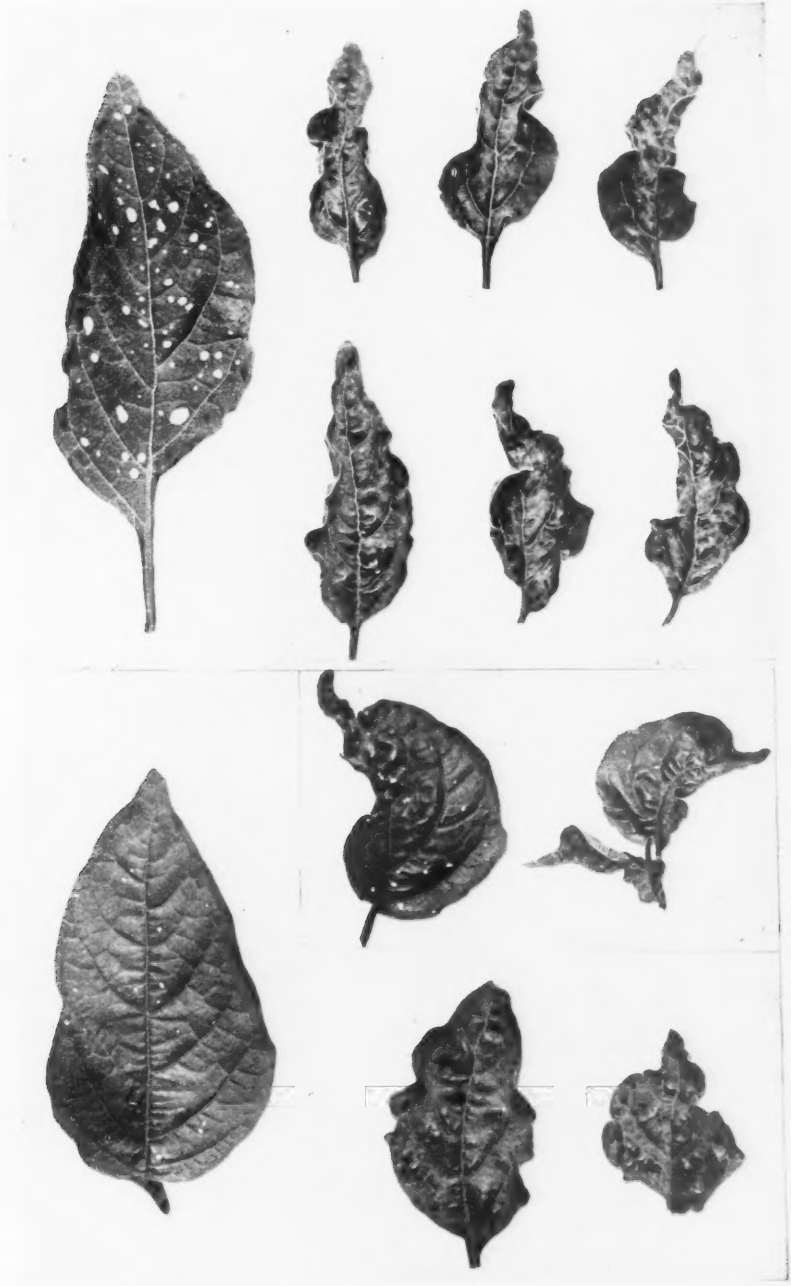

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EXPLANATION OF PLATE XVII

Symptoms of mosaic in *Physalis subglabrata:* at left two leaves from normal plant; at right ten leaves from mosaic plants; small holes in leaves eaten out by flea-beetles.

STROMA AND FORMATION OF PERITHECIA IN HYPOXYLON

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 296

PATSY LUPO

(WITH PLATE XVIII AND SEVEN FIGURES)

Hypoxylon and its allies have been left more or less uninvestigated on account of the coriaceous structure of the stroma and the difficulty of cutting satisfactory thin sections. DE BARY gave a general summary of FUISTING's researches on *Hypoxylon* and other members of the family, and said that it agreed with *Xylaria polymorpha* in the structure of stroma and the development of asci. He also stated that there appeared in the young coil that is the primordium of the perithecium "a row of broad cells irregularly rolled up and full of protoplasm," called by FUISTING Woronin hyphae. As the perithecium grows, these disappear by gelatinization, and the ascogenous hyphae, the periphyses, and the paraphyses grow out from a subhymenial layer of 6–8 cells that line the perithecium. The whole ascocarp, according to DE BARY, is filled with a mass of paraphyses before the ascogenous hyphae appear at their base and grow up between them.

In recent years only two of the family Xylariaceae have been studied, *Poronia punctata* by DAWSON,[1] and *Xylaria* by BROWN.[2] In that part of his study related to the development of the perithecium, BROWN says that in the center of a tangle of hyphae smaller than the others there are broad cells shorter and richer in protoplasm. These he identifies as Woronin hyphae, and states that they enlarge and probably divide, and then round off to form the large multinucleate ascogonia which usually fall to the bottom of the perithecium and there bud out the ascogenous hyphae. He further

[1] DAWSON, MARIA, On the biology of *Poronia punctata*. Ann. Botany **14**: 245–260. 1900.

[2] BROWN, H. B., Studies in the development of *Xylaria*. Ann. Mycologici **11**: 1–13. 1913.

states that paraphyses arise by an increased growth from the cells of the inner perithecial wall. The nuclear program, although not clear, is thought to involve an increase in the number of nuclei from the first uninucleate Woronin hyphae, and probably also further division in the ascogenous hyphae. From the comparative size of the nuclei he inferred fusion in the ascus, and this was the only fusion occurring in the life history.

Material and methods

The material used was collected in September from dead beech bark at Sullivan, Ohio, by Professor CHAMBERLAIN, who noticed that it seemed soft when all the other stromata around it were characteristically hard and mature. Specimens were sent to Mrs. FLORA PATTERSON, mycologist at the Bureau of Plant Industry in Washington, and she identified the form as *Hypoxylon coccineum*. It was fixed in chromoacetic acid and stained in haemotoxylin. Some of the material, which had not been satisfactory in safranin, was destained and then run into haemotoxylin; and some of the very young material was counterstained in gold orange. Both of these latter methods gave good results, because they differentiated the fungus cellulose and outlined the hyphae sharply, yet left the nuclei clear black and sharply marked. The sections were cut 2, 3, 4, 5, 8, and 10 μ thick, the younger stages being cut very thin. Whether or not the late fall development of this stroma is usual is not known to the writer.

Description of stroma

In longitudinal section (fig. 1) the stroma of *Hypoxylon* shows a differentiation into four distinct regions that can be seen in thin sections even with the naked eye. These are (1) an innermost central region, round in shape, which under the microscope is marked by a loose arrangement of hyphae emerging from the substratum; (2) a compacted zone above this of large, parallel, mostly empty hyphae that form a dome over the central region and up the main body of the stroma; (3) the perithecial layer of loosely woven hyphae with much interhyphal space and perithecia scattered throughout the region; and (4) the superficial layer which is further differentiated into a line marking off the fruiting zone by

intertwining hyphae running parallel to the stroma and taking a very dark stain, a space occupied by loose hyphae with dense protoplasmic contents, and a bounding surface of close hyphae staining black and doubtless containing the remnants of conidiophores.

In the central region three types of hyphae are distinguishable. The most conspicuous of these (fig. 2) is the one of large long cells

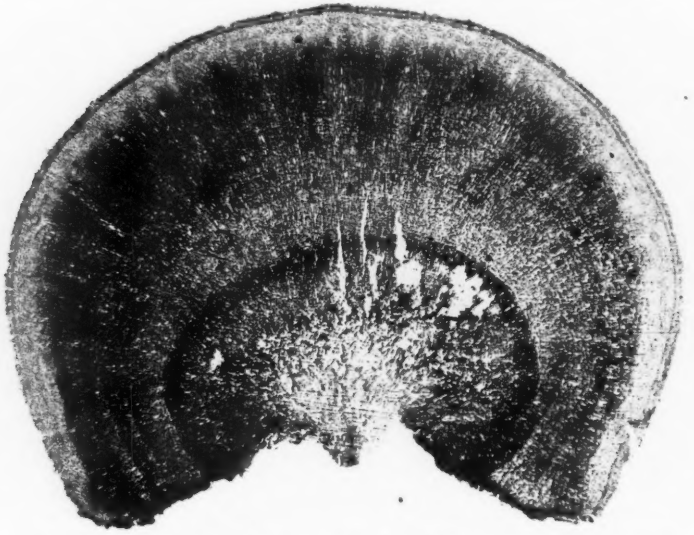
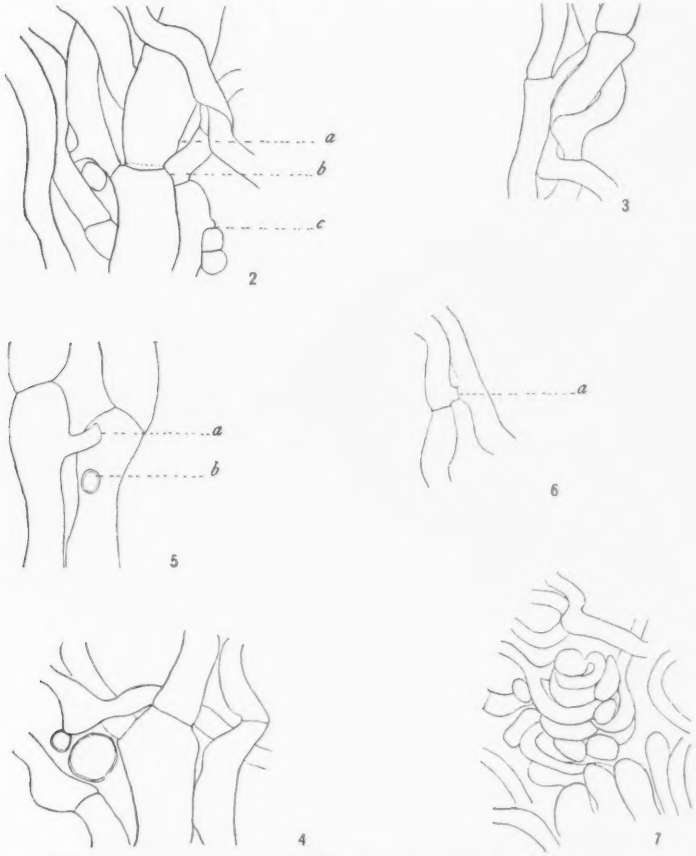


FIG. 1.—Longitudinal section showing borders of the four zones of stroma and the additional markings seen in compact layer of stroma; perithecia visible in fruiting zone; ×26.

staining brown, between which are small hyphae with dense protoplasm, and still smaller ones not staining so densely. These are apparently differentiated from the time of emerging from the substratum into stroma-forming hyphae, into hyphae which form the perithecium, and into those which form the conidiophores and superficial layers. The supporting structure is formed entirely by the largest filaments by means of various devices for interlocking the whole mass and giving to the stroma sufficient firmness, and the same devices are used also in the zone above this. One of the

most frequent devices is that of specially adapted articulation surfaces near the cross-walls (fig. 2*b*), where the cell of another



FIGS. 2–7.—Fig. 2, portion of hyphae from central region showing two principal variations in size and methods of mechanical support; *a*, pit through wall; *b*, articulation surface at septum; *c*, bulbous swellings and depressions fitting together; ×1250; figs. 3, 4, hyphae from same zone showing support gained by twisting and branching; ×1250; figs. 5, 6, interhyphal connections: *a*, bordered hole from sectioning protuberance; ×1250; fig. 7, surface view of early perithecial coil; ×1250.

thread rests against a flat supporting surface for a brace. Another method of support (figs. 2*c*, 3) is the interlocking of adjoining hyphae

by bulbous swellings from one cell fitting into corresponding depressions of the next. Sometimes the fungus thread branches dichotomously and forms a rest for another hypha in the fork (fig. 4), and again the two often intertwine and bend around each other (fig. 3). Contrary to expectation, the walls of the three types of hyphae are uniform in thickness, and although irregular thickenings of cellulose in the walls of the stroma-forming hyphae make them uneven, they are not really thicker. Pits (fig. 1*a*) through the walls are abundant, and although in a few rare cases these seem to be open, in the great majority a definite separating membrane is very clear. The cells of the smaller hyphae are binucleate, but the nuclear condition in the larger is difficult to distinguish, because in the few places where the contents are visible they contain dark-staining granules. As definitely as could be distinguished, however, they have many multinucleate cells which have probably developed from the binucleate condition by division of the nuclei.

In the compact zone above the central region the stroma appears to be uniformly composed of the same large empty-celled hyphae already mentioned, which radiate out in parallel rows from the center to the periphery; but if the filaments are spread apart or a cross-section is examined the same differentiation of the three sizes is seen. The walls show the same thickenings and pits already described, and the cells fit into each other in the same way, making a very firm dense pseudoparenchyma. In some places, beside the incurving of cells to each other, they hold together in the corners, much like xylem cells. One peculiarity of this part of the stroma seen in longitudinal section is the large number of holes bordered by walls (fig. 5*b*). These are cut ends of protuberances from the cells (figs. 5, 6), and are one of the methods of mechanical support not found in the previous zone. They are not the technical clamp connections of DE BARY'S description, because they occur not only near the septa, but from any place along the cell to another in the same hypha, and because they cannot be so named until their method of development has been established. Here they are blind tubes that reach from one cell to fit flat against the wall of an adjacent hypha and clamp the two together.

Other peculiarities of this part are the brown mottled appearance of the whole region, due probably to irregular depositing of some substance in the walls, and the further zonation of this portion of the stroma (fig. 1). This last character is one of the peculiar taxonomic features of *Daldinia*, and in *Hypoxylon* is not evident except through the microscope. These parallel markings are due to irregularities in growth that result in a region of short cells bordering a region of long cells, and to the hyphae intertwining more at this point.

On the outer edge of this portion of the stroma the large hyphae end at varying levels, sometimes with a club-shaped enlargement, and do not give a definite line of demarcation. From between these the two types of hyphae rich in protoplasm pass out to form the upper layers, and of these the larger do not pass much beyond the lower part of the perithecial zone, where some of them form the fruiting bodies, and the smaller continue on beyond this to form the three superficial boundaries. It is this situation which indicates that the sizes of these hyphae were differentiations according to function and not accidental variations. In this region of scattered hyphae that form the perithecial layer, and also in the three outer regions, the cells are typically binucleate, although a very few with several nuclei are seen; and this is true also for the hyphae forming the perithecial wall. On the outer surface of the stroma are spherical excrescences like bubbles, and these are related to the interhyphal spaces. They are probably the excretion of some oily substance through the stroma, and it is owing to this that the young stromata feel smooth and slightly greasy to touch.

Formation of perithecia and ascogonia

In the formation of perithecia in *Hypoxylon* the first evidence of their origin is the coiling of hyphal ends or of branches. As already stated, it is the larger of the two protoplasm-filled hyphae differentiated from the substratum that do this, and apparently they do not show any increase in size before or immediately after this stage. Other hyphae of the same size surround these initial coils and form a small circular knot (figs. 7–9), which was the earliest stage BROWN recognized in the development of the perithecia in

Xylaria. From the evidence there is no basis for believing in any earlier differentiation of Woronin hyphae as initiating the coiling process; but they do become differentiated in the center of the coil by an increase in size very soon after the perithecial primordia are well started (fig. 10). Growth in the size of the perithecium is accomplished by increase in the length of the wall hyphae, and also by the addition of other hyphae around the outside. With this increase in size the wall layers become thinner and compact, and some of the inner hyphae decrease in size and become absorbed, probably furnishing nourishment for the fertile branches (figs. 10, 11*d*). A large number of perithecia start but few mature, and these, logically in relation to their food supply, are mostly toward the inner line of the perithecial zone. The others remain intact and are scattered throughout the fruiting region, apparently inhibited from further growth at any stage in their development, and remaining without change at that stage. As an exception to this, some of the larger perithecia that have reached the point where they contain ascogonia and then become abortive show signs of deliquescing and disintegrating. As a rule the older perithecia are toward the top of the stroma and the younger stages are down toward the substratum.

Within the perithecium the filament in the center develops into the Woronin hypha (fig. 10). It increases in length, and in size and number of cells; and after this some of the cells round out, increase in size, and eventually separate from each other to form the ascogonia. The enlargement is not uniform as to the size and shape attained, for these ascogonia (fig. 11*b*) are many of them uneven and contorted in outline, and many of them retain narrow stalklike connections with cells from which they have not become completely separated.

The nuclear condition in the Woronin hyphae and ascogonia is the critical point, and is hard to determine because of the extreme variations in the size of the nuclei and the difficulty of determining successive stages. As said before, the cells of the Woronin hyphae are binucleate (fig. 9), and as they enlarge (fig. 10) they show a steady and marked increase in the size of the nuclei from the time the knot is well formed. There are one or two divisions, after

which they increase their size, and at the time of the rounding out of the ascogonia there are four, sometimes more, large nuclei five or six times the size of the originals. As the ascogonia increase to the enormous odd shapes found in the more mature perithecia, the nuclei show great variation in size and number (fig. 11). During this stage they undergo rapid division without maintaining their size, and in the ascogonia which show evidences of budding out the ascogenous hyphae they are small and number sixteen or more in a section. Evidence for this interpretation of the nuclear program is gained also from the perithecial wall, because as it grows more mature in character these changes in size and number are unmistakable. There is no evidence of fusion in any stage of the development of the ascogonia. No mitotic figures were visible, but in many cases the position of the two nuclei was such as to suggest late division.

The ascogonia do not drop to the bottom of the perithecium before germinating. Instead the increase in size of the wall is toward the periphery of the stroma, and the ascogonia, although in the same actual position, seem to have dropped because of the expansion of the perithecial wall toward the surface.

Ascogenous hyphae

The material used was just at the stage when the ascogenous hyphae were beginning to bud out, and no detail about the formation of these can be given. Great care was necessary not to confuse some of the stalk connections where separation was incomplete with ascogenous hyphae. These could be recognized by their direction and evident connection with some part of the filament traced through serial sections. Legitimate cases of buds (figs. 12, 13) just formed were found, however, and although of course the nuclear situation, separation, and branching could not be determined, apparently the procedure would be the same as described for other forms where the nuclei migrate into the buds from the ascogonia, and further division takes place there.

A supposition lacking evidence to support it is that the paraphyses described by DE BARY and BROWN might be formed from these early ascogenous hyphae or branches of them instead of

from a subhymenial layer. This seems reasonable, since at this stage the compact wall of the perithecium is an unlikely place for new growth, and there is no evidence of new hyphae being found to account for the paraphyses in other forms. It seems very probable that this is their origin here.

Summary

1. The stroma is differentiated into four regions, and in one of these further zonation is evident.

2. The firm structure of the stroma is gained by various mechanical devices for support, such as tubular extensions from cells, branching and intertwining of hyphae, and special articulation surfaces.

3. The hyphae are differentiated into three types from the time of their emergence from the substratum: those that form the major part of the stroma, those that form the perithecia and Woronin hyphae, and those that form the superficial layers and probably the conidiophores.

4. The cells of the hyphae are originally binucleate, but may become multinucleate.

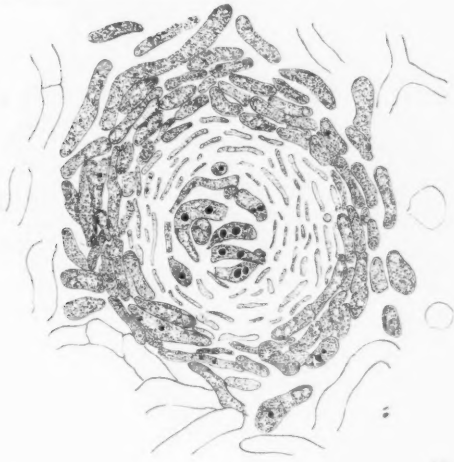
5. The formation of the perithecia is initiated by the massing of the hyphae into a circular knot, within the center of which the Woronin hyphae differentiate.

6. The ascogonia develop from the cells of the Woronin hyphae by rounding out, partially separating from each other, and increasing in size.

7. The ascogonia do not drop to the bottom of the perithecium in the older stages, but come to lie comparatively closer to the bottom by an expansion of the perithecial wall toward the periphery of the stroma.

8. The nuclear program within the ascogonia is one of few divisions and great increase in size, up to the stage where the ascogonia are well rounded out, and then of rapid division without the maintenance of size.

9. The ascogonium buds out protuberances that are the beginnings of the ascogenous hyphae.



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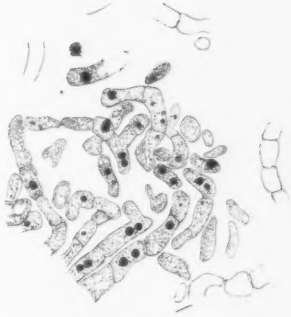

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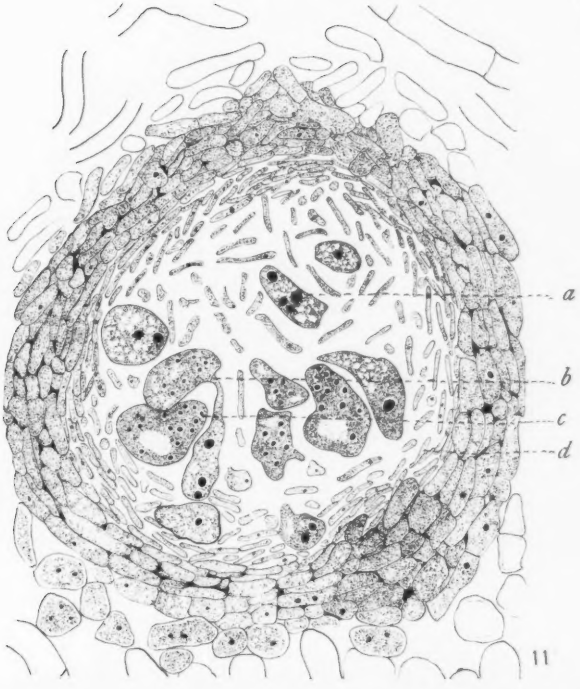

11

13

LUPO on HYPOXYLON

The writer wishes to express appreciation and thanks to Professor C. J. CHAMBERLAIN, under whose direction the study was made; and to Mrs. FLORA PATTERSON for identifying the material.

ROCKFORD COLLEGE
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EXPLANATION OF PLATE XVIII

FIG. 8.—Early stage of coil in section, showing nuclei already increased in size; ×1375.

FIG. 9.—Another view of approximately same stage, including several cells with nuclei of original size; ×1562.

FIG. 10.—Later stage of perithecium with wall yet loosely formed: large nucleated Woronin hyphae in center of perithecium; ×1562.

FIG. 11.—Still later stage with compacted wall and growth toward periphery started so that ascogonia lie relatively nearer bottom: *a*, large nucleated ascogonium; *b*, ascogonia of irregular shape and stalklike connection left with what was original coil; *c*, multinucleate mature ascogonium; *d*, hyphae decreasing in size and disintegrating; ×1562.

FIGS. 12*a*, 13.—Beginning stages in budding of ascogonia to form ascogenous hyphae; ×1562.

CURRENT LITERATURE

NOTES FOR STUDENTS

Quantitative relations of regeneration.—REED[1] has contributed a new quantitative study of growth in pruned trees as compared with unpruned, with particular reference to such questions as whether the growth response is merely the restoration of lost parts, in what manner the amount of regeneration is correlated with length, and number of buds of the mother shoot; also what light these relations afford in the problem of the dominance of the shoot apex. He finds no correlation between the length of mother shoots and the amount of new growth produced by them, whether pruned or unpruned. On the other hand, shoots pruned the previous winter produced about 65 per cent more total growth than comparable unpruned shoots; the degree of heading back had little effect on the amount. Hence, regeneration following pruning is not a tendency to restore lost parts, but in terms of growth rate of the shoot is taken to indicate increased activity of the growth catalyst. In connection with the characteristically greater growth of laterals at the distal end of a pruned shoot, the conclusion is reached that this greater activity results from the elimination of the growth-inhibiting chalones produced in the apical part of the shoot which normally keep the lateral buds in dormancy. The alternative hypothesis that pruning reduces the number of potential growing points, hence permits of greater development of the remaining buds, is rejected because it was found that the more heavily pruned mother shoots, that is, the shoots in which the number of remaining buds was least, failed to make more total lateral growth than the longer mother shoots. It is worthy of note that according to the author's hypothesis of basipetal migration of a growth-inhibiting substance, the greatest concentration, and hence the most pronounced inhibiting effect, is at the base of the shoot. When a mother shoot is pruned to a few basal buds, however, the laterals developing from such buds become longer than laterals of less severely pruned shoots. This would seem to be evidence indicating some effect from reduction of competition between the several buds.

LOEB[2] reaches a somewhat different conclusion from experiments on regeneration in *Bryophyllum*, in which the weight of shoots produced from the

[1] REED, H. S., Correlation and growth in the branches of young pear trees. Jour. Agric. Res. **21**:849–876. *pl. 1.* 1921.

[2] LOEB, JACQUES, The quantitative basis of the polar character or regeneration in *Bryophyllum*. Science **54**:521–522. 1921.

apical buds of an intact defoliated stem was compared with the total weight of shoots produced from similar stems divided into portions of one node each. From the approximate equivalence of these quantities he concluded that "the polar character of the regeneration of shoots is due to the fact that all the material available for growth reaches the apical and none of the other nodes of a long piece of stem." The relation of this conclusion to LOEB'S well known earlier work on regeneration in *Bryophyllum* is not quite clear to the reviewer, since nothing appears here concerning the effect of a growth-inhibiting hormone by which is to be explained the dominance of the apical and the inhibition of the lateral buds.

Although the reviewer is aware that the two cases are not strictly comparable, it would seem that if inhibition of lateral buds is the effect of a basipetally migrating growth-inhibiting substance, the maximum effect of "pruning" would result from complete isolation of each bud from the deleterious effects of its neighbors, as LOEB was able to do in *Bryophyllum*, and as was impossible in REED'S experiments with the pear. Yet the experiment with *Bryophyllum* resulted in the production of a greater amount of new growth from the intact than from the divided stem.

The arguments in support of the several theories to account for the dominance of the apical portion of a shoot have been reviewed recently by CHILD,[3] and several objections to the hypothesis of growth-inhibiting hormones pointed out. It would appear that further progress toward the solution of this problem must wait on more adequate information concerning the anatomical relations of apical and lateral buds, and of tissue changes in regeneration. For instance, the transport efficiency of the vascular supply to the apical as compared with lateral buds does not appear to have been adequately investigated. The relative age of the terminal as compared with other buds is important in this connection. In shoots with the indeterminate growth habit the apical bud may establish its dominant rôle in the axial gradient, which it thereafter retains, in the judgment of CHILD, by virtue of its priority. In shoots of limited apical growth different relations may obtain. Again, if inhibition of a growing tip is a transmission through protoplasmic connections rather than the physical transportation of a substance through the vascular tracts, as CHILD holds on the basis of the behavior of simple animals and non-vascular plants, evidence of cytoplasmic cell connections should be sought in such active portions of the shoot. The effect of callus deposition in the sieve tubes and of changes in the phloem (both sieve tubes and parenchyma) toward lignification should be determined in relation to a possible gradient in transport efficiency from apex to base. The coordination of histological and physiological studies in this problem is greatly to be desired.—FREEMAN WEISS.

The rapprochement in ecology.—A notable feature in the development of ecology has been the marked divergence between the American and Continental

[3] Amer. Jour. Bot. **8**: 286–295. 1921.

European schools. Continental ecology, developing naturally and by degrees from the older study of floristic plant geography, has retained much of the taxonomic standpoint, and methods for distinguishing, classifying, and arranging vegetational units according to their physiognomy have been very highly developed. In America, on the other hand, and latterly also in the British commonwealths, the tendency has been much more to emphasize the dynamic and genetic aspects, especially under the leadership of COWLES, in the development of the successional idea. The quadrat method of POUND and CLEMENTS, to be sure, was a notable contribution to physiognomic ecology, but CLEMENTS became an early convert to the successional doctrine, and has been one of its most voluminous exponents. Thus the Anglo-Americans and the rest of the world have come to present united and opposing fronts, and the situation has become sufficiently tense to induce the remark from ROMELL,[4] "Entre divers partis des phytogéographes la divergence grandit, on pourrait déjà dire la lutte s'enflamme." The first part of his statement is true enough, and the latter part could easily have become so, if the one side had been as willing to accept battle as the other was to offer it. It goes without saying that such a situation is a most regrettable one for the science of ecology. It is encouraging therefore to note, in a group of recent Continental papers in ecology,[5] a markedly increased toleration of the successional-dynamic point of view, as well as indications that physiognomic methods may yet be developed that will not seem too metaphysical in conception and too unwieldy in practice for the American temperament.

RÜBEL'S three papers are especially valuable as a comprehensive and highly condensed summary of the progress of ecology. He traces the early growth of the science, from the vague first beginnings with THEOPHRASTUS and the more or less disconnected comment of early modern taxonomic botanists, through its evolution as a subspecies of phytogeography, to its present and independent development. The history of the numerous efforts to arrive

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[4] ROMELL, LARS-GUNNAR, Physionomistique et écologie raisonnée. Svensk Botanisk Tidskrift **14**:136–146. 1920.

[5] RÜBEL, EDUARD, Anfänge und Ziele der Geobotanik. Vierteljahrsschr. Naturf. Gesells. Zürich **62**:629–650. 1917.

———, Über die Entwicklung der Gesellschaftsmorphologie. Jour. Ecol. **8**:18–40. 1920.

———, Die Entwicklung der Pflanzensoziologie. Vierteljahrsschr. Naturf. Gesells. Zürich **65**:573–604. 1920.

BRAUN-BLANQUET, J., Prinzipien einer Systematik der Pflanzengesellschaften auf floristischer Grundlage. Jahrb. St. Gallischen Naturw. Gesells. **57**:305–351. 1921.

FITTING, HANS, Aufgaben und Ziele einer vergleichenden Physiologie auf geographischer Grundlage. pp. 42. Jena. 1922.

PALMGREN, ALVAR, Die Entfernung als pflanzengeographischer Faktor. Acta Soc. Fauna et Flora Fennica. **49**:no. 1. 1921.

at some satisfactory method for quantitative estimation of vegetational values is of particular interest. The methods of the earlier workers were heterogenous and often confused. Later methods gained in the matter of clarity of ideas, but were highly complicated and exceedingly laborious. Present day effort is toward simplification, and in this the work of RAUNKIAER and BRAUN-BLANQUET is perhaps most promising. The latter's paper, in addition to the effort toward clarification and simplicity, just mentioned, is notable for its proposal to classify his plants also according to their dynamic value, that is, in American terminology their successional value. He proposes a series of five valuations to be applied to the species in any given association, together with symbols for their convenient designation. His class names, with approximate English equivalents, are aufbauend (constructive), erhaltend (maintaining), festigend (consolidating), neutral (neutral), abbauend, zerstörend (disruptive). The idea of progressive and regressive succession is thus clearly postulated.

The ecological implications in FITTING'S contribution are all the more valid in that they are not directly intended. The author is a physiologist, and his primary concern is the avoidance of the artificial and abnormal conditions imposed on his material by the greenhouse methods of ordinary laboratory practice. He contends that the physiology of plants should be studied where the plants naturally occur, and insists on the study of climatic, edaphic, and biotic factors as they affect the space actually occupied by the plant in the field. This, of course, coincides with the activities of the younger American ecologists who are carrying physiology out of doors.

PALMGREN'S study is one of migration, and thus implies the successional viewpoint throughout, it is the more noteworthy in that it was conducted on the Aland archipelago, almost within sight of Uppsala. These islands, he estimates, have not been emerged for more than 3500 years; moreover, they are high-boreal in position, so that an ecologist with the successional viewpoint can extract much aid and comfort from his conclusions.

All this is gratifying to Americans, but as yet there is not much indication of reciprocity on our part. FULLER and BAKKE anticipated the German publication of RAUNKIAER in making his ideas accessible to the English-reading public, but little or nothing has been done in this country with his methods. Probably most American ecologists feel that still further simplification is needed. RAUNKIAER himself admits that his methods involve a good deal of labor. Then there is also the element of time; it generally takes about two graduate "generations" to establish a new idea.—FRANK THONE.

Stomatal regulation.—Using LLOYD'S methods of studying stomata, which he thinks have been criticized without sufficient reason, LOFTFIELD[6] has made

[6] LOFTFIELD, J. V. G., The behavior of stomata. Carnegie Publ. no. 314. pp. 104. 1921.

an extensive study of diurnal stomatal changes, the influence of physical factors on the opening and closing of stomata, and the effects of these stomatal movements on transpiration. The main observations were made on alfalfa, potato, sugar beet, onions, and cereals, but some sixty species in all have been examined. He finds three types of stomatal behavior: the cereal type, typified by barley; the thin-leaved mesophyte type, typified by alfalfa; and the fleshy-leaved type (not confined however to plants with fleshy leaves), typified by such plants as the potato, cow beet, and onion; each of these has a different closure reaction to extreme conditions. The cereals show no opening of stomata at night, no matter how slight the opening by day has been. The thin-leaved mesophytes have the stomata usually open by day and closed at night, but under extreme conditions show a closure during the middle of the day, correlated with an opening at night. The thick-leaved plants behave much as marsh plants do, having their stomata open day and night when water content is high and evaporation low, and showing a tendency to close only when the evaporating capacity of the air is high.

Many details regarding the effects of environmental changes, such as light intensity, temperature, evaporation, wind flow, water content of soil, leaf turgor, and habits of growth on stomatal behavior are presented, from which one may draw the general conclusion that stomata are sensitive to environmental conditions, particularly to light, and to factors that reduce the water content of the leaf, and that they open and close as conditions necessitate. The evaporation studies indicate that atmometers and potometers do not measure accurately the total effect of evaporation factors upon plants, a result that is not surprising.

The final section on the effect of stomatal movement upon transpiration throws much light on the mooted question as to whether stomata exert a regulatory function in transpiration. LLOYD had concluded in 1908 that stomata have no regulatory function, a conclusion which was rendered doubtful by several investigators, including ILJIN, who studied the transpiration of mesophytes and xerophytes in ravines and on the Russian steppes, and who found marked evidences of regulation of transpiration. This work by LOFTFIELD seems to settle the question definitely in favor of stomatal regulation, particularly when the apertures are nearly closed. As long as the apertures are more than 50 per cent open, the transpirational water loss is controlled by evaporation factors alone, but with closure almost complete, the stomata regulate very closely the water loss from the plant. The paper is beautifully illustrated with plates showing photomicrographs of stomata.—C. A. SHULL.

Anthocyan pigments.—NOACK[7] has found rhamnose-free flavonol diglucosides to be much more abundant in green leaves than has generally been supposed. In such leaves as he studied he was able to establish the existence

[7] NOACK, K., Zeitschr. Botanik **14**:1–74. 1922.

of flavonol-anthocyan in couples of similar glucosidal nature, but secured no evidence of aromatic nucleus composition in such cases. He suggests that these couples function as a reduction mechanism during photosynthesis.

WHELDALE[8] had already indicated reasons for believing anthocyan formation associated with photosynthetic defect. NOACK'S work strengthens this view. He finds fluorescent media in the presence of light capable of oxidizing anthocyanins to flavonols, and a general inverse relation between chloroplast integrity and anthocyan content. Especially has he shown that absence of carbon dioxide will cause anthocyanin formation in sunlight, and that engorgement with sugar probably acts indirectly (he thinks by disturbing the photosynthetic mechanism) in producing anthocyanins. That there are serious gaps in his work he has been the first to admit. He has, however, given added dignity to a point of view which comes surprisingly close to harmony with much of our knowledge. The action of narcotics, low temperatures, high insolation, and ultraviolet light, nitrogen and phosphorus starvation, as well as extremes of youth and senescence in photosynthetic organs, certainly fall in line with such a conception in a most disarming way.

The formation of anthocyanins by reduction from flavonols, as well as WILLSTÄTTER'S[9] general scheme for color change, are elucidated by EVEREST and HALL[10] in a trenchant reply to the paper of SHIBATA, SHIBATA, and KASIWAGI.[11] It will be recalled that the latter workers attribute color conditions to metal organic or complex compounds of reduced flavonol glucosides, rather than to alkaline phenolic salts, free stages, and red oxonium salts of anthocyanins. In the present paper strong evidence is adduced that this contention is based upon work with supposedly pure substances which were actually mixtures, and the resultant analyses are pronounced of no value. It is interesting to note that EVEREST and HALL now believe blue flower pigments to be of two general types, the alkali phenolic salt of anthocyan, which polymerizes to colorless on standing, and the iron double salt, stable in dilute solution. They have also demonstrated the existence of flavone substances in a number of very young buds previous to anthocyan formation, but have failed to find anthocyans preceding flavone formation in flavone-holding organs.

There can be little doubt that botanists are now ready to look with the keenest interest toward precise chemical comparisons of flavone and anthocyan pigments wherever the two are found associated, whether simultaneously or in sequence.—PAUL B. SEARS.

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[8] WHELDALE, M., The anthocyan pigments of plants. 1916 (p. 81).

[9] WILLSTÄTTER, R., and EVEREST, A. E., Liebig's Ann. Chem. **401**:189–232. 1913.

[10] EVEREST, A. E., and HALL, A. J., Proc. Roy Soc. B **92**:150–162. 1921.

[11] SHIBATA, SHIBATA, and KASIWAGI, Jour. Amer. Chem. Soc. **41**:208. 1919.

Ecology of heather.—One of the most commendable features of modern ecology is seen in the present tendency to focus attention on some particular plant which is examined as to its responses and limitations. A notable example of this type of investigation is seen in Miss RAYNER's studies of *Calluna vulgaris*. In a preliminary paper[12] she pointed out that while the plant has been regarded as a typical calciphobe, it occurs in sharply defined communities on the chalk downs in Wiltshire and Berkshire, and appears able to compete with the vegetation characteristic of the downs. According to this investigation the heather communities appeared limited to a heavy rich loamy soil relatively high in magnesium content and neutral in reaction. Beyond these communities there was a poor chalk soil with 40 per cent of calcium carbonate.

An examination of the germination and seedling habits of *Calluna*[13] showed that the seedlings developed normally upon the soil from the heather areas and abnormally upon the chalk soil. Upon the latter the germination was reduced and retarded, the development of the root and shoot arrested, and the leaves were small in size and red in color. The seedlings were found to be infected with a mycorhizal fungus shortly after germination, the mycelium coming from the seed coat which seems to have been infected while still in the ovary. Seed can be sterilized with no effect upon germination, but in the absence of infection complete arrest of root formation occurs, showing the relation of *Calluna* to the root fungus to be obligate.

A further examination of this symbiosis,[14] already noted in this journal,[15] proved even more conclusively its obligate character and the absence of root development in sterile cultures. The fungus was found to be present in all parts of the plant infecting the testa, but not the embryo and endosperm of the seed. The fungus was isolated, grown in pure cultures, and sterile seedlings were inoculated with resulting normal development.

In the most recent contribution Miss RAYNER[16] has succeeded in demonstrating by experimental cultures that *Calluna vulgaris* will not grow on calcareous soils because of an inimical factor, chemical in nature, present in such soils. The exact chemical character of this factor is as yet unknown, but it seems probable that it is effective by altering the infectibility of the root cells of the seedlings and their relations with the mycelium after infection. It does not seem to affect the fungus when growing outside the plant.—GEO. D. FULLER.

[12] RAYNER, M. C., and JONES, W. N., Preliminary observations on the ecology of *Calluna vulgaris* on the Wiltshire and Berkshire Downs. New Phytol. **10**:227–240. *figs. 2.* 1911.

[13] ———, The ecology of *Calluna vulgaris*. New Phytol. **12**:59–76. *pl. 1. figs. 2.* 1913.

[14] ———, Obligate symbiosis in *Calluna vulgaris*. Ann. Botany **29**:97–153. *pl. 6. figs. 4.* 1915.

[15] BOT. GAZ. **60**:166. 1915.

[16] RAYNER, M. C., The ecology of *Calluna vulgaris*. II. The calcifuge habit. Jour. Ecol. **9**:60–74. *pl. 1.* 1921.

Cytology of Neottia Nidus-avis.—A paper by MODILEVSKI,[17] dated 1918, has just reached this country from Kiev, Russia. The paper is in Russian, but has a rather complete summary and an explanation of figures in English. The cytological part deals principally with the behavior of the chromatin during the two reduction divisions in oogenesis. Particular attention was given to the character of the spirem thread, and the conclusion was reached that no true double structure is present either before synapsis, during synapsis, or immediately after, although in rare cases a parallel orientation could be seen in the late spirem stage. Before the diakinesis stage is reached, a double character is easily observed, and eighteen bivalent chromosomes are formed, some of which are larger than others. One of the bivalents is much longer than the rest, and is conspicuous during the subsequent stages of division. MODILEVSKI believes that in structure the chromosomes are masses of threads, and that there is no vacuolization, like that described by GREGOIRE and many others. Besides the long chromosome, there are three others which are morphologically different from the remaining fourteen chromosomes; however, he does not seem to think that this situation has any serious value for theoretical considerations. Reduction was also studied in the pollen mother cell.

Some attention is given to the nucleolus, which he thinks consists of two distinct morphological and chemical constituents. One element is the permanent nucleolus, which stains with iron-haematoxylin, and is identical with the nucleolus of somatic nuclei. The second has the shape of a sickle and rests upon the other like a cap. It stains like chromatin. These two kinds of nucleoli always appear during late synapsis in *Neottia Nidus-avis*. During the two reduction divisions of the megaspore mother cell no walls are formed, and all four megaspores take part in the development of the embryo sac. The two antipodal nuclei do not divide again, but the other two enlarge and divide, so that there are four nuclei at the micropylar end of the sac. They develop a typical egg apparatus and a polar nucleus. One of the male nuclei fuses with the egg nucleus and the other with the micropylar polar nucleus. As the young embryo develops, four free nuclei are found in the embryo sac, one of them a synergid nucleus, the two antipodal megaspore nuclei, and the nucleus formed by the fusion of a sperm with the micropylar polar nucleus. There is no free nuclear division or any formation of endosperm.—C. J. CHAMBERLAIN.

Sporidial infection in Puccinia graminis.—A recent contribution to the series of studies in the physiology of parasitism emanating from the Imperial College of Science and Technology (London) is by WATERHOUSE,[18] describing

[17] MODILEVSKI, J., Cytological and embryological studies on *Neottia Nidus-avis*. pp. 55. *pls. 1, 2.* 1918.

[18] WATERHOUSE, W. L., Studies in the physiology of parasitism. VII. Infection of *Berberis vulgaris* by sporidia of *Puccinia graminis*. Ann. Botany **35**:557–564. *figs. 19.* 1921.

host penetration by the sporidial germ tube of the cereal stem rust fungus. Although ERIKSSON studied sporidial infection in the mallow rust, concluding that penetration is directly through the epidermal cell wall and never through stomata, no careful study of the mechanism of entry of the sporidial germ tube has previously been made. In the present account penetration is shown to result from mechanical action alone, the structures concerned in the process being a mucilaginous investment of the germ tube and a fine style-like infection hypha, originating either from the germ tube or the sporidium directly. The entry of the parasite at first causes no visible alteration of the host cell contents. This manner of parasitic entry, that is, in the absence of visible chemical softening processes of the cuticle, is similar to that previously reported for the infection hypha of *Botrytis* and *Colletotrichum*, and for the zoospore of *Synchytrium* (CURTIS). A new interest is thereby given to studies of disease resistant or disease escaping plants directed toward the mechanical properties of the cuticle and cell wall. Evidence that resistance to infection of potato by *Pythium debaryanum* is of this type has already been presented (HAWKINS and HARVEY); similarly for resistance in the tomato to infection by *Macrosporium tomato* (SANDO and ROSENBAUM).

The question is pertinent whether the resistance or immunity shown by different species of *Berberis* to infection by *Puccinia graminis* is due to mechanical exclusion of the germ tube by a heavy cuticle. There is some evidence that this may be true for the evergreen thick leaved species of *Berberis* generally referred to *Mahonia* or *Odostemon*. Greenhouse inoculations with several forms of *Puccinia graminis* have resulted in infection of very young leaves of *Berberis trifoliolata*, *B. Fremontii*, and the tall form of *B. Aquifolium*=*Odostemon Nutkanus* (DC) Rydb., although on the last named host only abortive pycnia and no aecia developed. Some other factor appears to be concerned in the immunity of *Berberis Thunbergii* to cereal stem rust, since this plant has soft, thin leaves which lack a well developed cuticle.—FREEMAN WEISS.

Further studies on Tmesipteris.—The life history of the Psilotales is becoming as well known as that of more accessible lycopods through the continued researches of HOLLOWAY,[19] who has published a second paper on the prothallus of *Tmesipteris*, containing additional observations made possible by the finding of more than 200 additional prothallia. *Tmesipteris* and *Psilotum* both have sporelings which resemble their gametophytes. This similarity is not considered by HOLLOWAY as being sufficient evidence for the primitiveness of the Psilotaceae; but he points out that this close correspondence is not found in the life history of other modern Pteridophytes. This resemblance between the two generations, the superficial position of the sex organs, the persistent single apical cell of the prothallus, the dichotomous

[19] HOLLOWAY, J. E., Further studies on the prothallus, embryo, and young sporophyte of *Tmesipteris*. Trans. New Zealand Inst. **53**:386–422. 1921.

branching, the absence of a primary tubercle, and the lack of differentiated tissue "may all be urged as more or less primitive features." The absence of a suspensor the author thinks may be compensated for by the haustorial protuberances of the foot. The same foot structure, however, also occurs in certain species of *Lycopodium* which do develop a suspensor. The absence of the suspensor is also counted as a primitive feature.

In discussing the significance of its embryogeny, which is "the simplest among existing pteridophytes," the author states: "While not suggesting that *Tmesipteris* has actually been derived from the *Anthoceros* cycle of affinity, it is clear that the absence from the former of any such organs as root or cotyledon suggests that they approximate in so far as they both represent primitive lines of development. That the simplicity of *Tmesipteris* is not due to reduction is a belief which has greatly been strengthened by the discovery of the rootless and leafless Rhyniaceae. The embryogeny of *Tmesipteris* as described in the present paper makes more clear-cut the theory of the origin of the sporophyte of the Pteridophyta from an *Anthoceros*-like sporangium. . . . . The only new feature to be postulated here is the extension in length of the shoot from an apical meristem instead of, as in *Anthoceros*, from an indefinite basal meristem, and the initial cause of the shoot-elongations might be set down as being the adoption of a subterranean mode of life by the gametophyte."—E. A. SPESSARD.

Life cycles of bacteria.—LÖHNIS[20] has published a comprehensive survey of the literature dealing with cell forms of bacteria and their significance in relation to the life history of these organisms. The discussion is amply illustrated with over 40 plates containing nearly 400 figures.

The first section of the monograph contains a discussion of cell forms. The author attempts to refute the monomorphistic doctrine of COHN, KOCH, and their followers. It is shown that many bacteria, possibly all, are pleomorphic, and that the varying cell forms often referred to as "involution" or "degeneration" forms are really different stages in the life cycles of bacteria. It is admitted, however, that our knowledge concerning the relationships of these forms is all too meager.

In the second section reproductive organs are discussed. These are gonidia, regenerative bodies, exospores and endospores, arthrospores, and microcysts. Of these the gonidia and regenerative bodies appear to take the most active part in reproduction, while the other organs may represent resting forms. It is claimed that gonidia are common to all bacteria. The fact that they have not always been observed may be due to their small size and high motility. Regenerative bodies may be of any shape, and are produced either by the vegetative cell or the "symplasm."

[20] LÖHNIS, F., Studies upon the life cycles of the bacteria. Part I. Review of the literature, 1838–1918. Mem. Nat. Acad. Sci. **16**: Second memoir. pp. 252. *pls. A–S* and *1–23*. 1921.

The third section of the monograph contains a discussion of this symplastic or amorphous state, in which it is claimed that all bacteria may live and from which new cells may form. The monograph concludes with brief discussions of "conjunction" and of methods of study. While LÖHNIS' discussion of pleomorphism is excellent, it must be admitted that the sections dealing with reproductive organs and with symplasm are not entirely convincing. It is at times difficult to follow his interpretations of the illustrations. At the same time, the monograph is very suggestive of lines of work which ought to be followed in the study of the life cycles of the lower organisms. Such investigations would be well worth while.—J. F. NORTON.

Mycorhiza of forest trees.—The conclusions of MCDOUGALL[21] that "the tree is not benefited by association with the fungus, and that the ectotrophic mycorhizas are not symbiotic associations, but are instances of the parasitism of fungi on the roots of trees," have caused some doubt of the importance ascribed to root fungi by FRANK and other earlier workers. A recent preliminary paper by MELIN,[22] however, indicates that in all probability MCDOUGALL was unwarranted in rendering so general a verdict, and while mycorhizas may be quite unimportant for many American trees, they nevertheless assist in the nutritive processes of certain species, and may be an absolute necessity for some, as recently shown by RAYNER[23] in the case of *Calluna vulgaris*.

In the present investigation MELIN has found that the mycorhizas of *Pinus silvestris* and *Picea Abies* cause a limited development of rootlets. In the former the dichotomous branching is often modified by the development of nodules as large as peas, composed of many densely crowded short branches. Three mycorhizal fungi have been isolated from the *Pinus* by this worker, and one from the *Picea*. They have been preliminarily called *Mycelium radicis silvestris* and *M. radicis abietis*. Their systematic position and internal relations are for the present left open. They are aerobic organisms growing more vigorously in an acid substratum, are exceedingly specialized, and develop slowly. No fixation of nitrogen takes place in pure cultures of the fungi, although there is evidence that the mycorhizas of *Pinus silvestris* fix the nitrogen of the air. Seeds of both these trees germinate without the fungi, and there is no dissemination of the fungi by the seed. The fungi from pure cultures infect sterile seedlings through root hairs, and the young plants then develop more vigorously. At first the hyphae grow principally in the interior of cortical cells, where they form a pseudoparenchyma of the same appearance as in the fungus mantle of the completely developed mycorhiza. Later the "Hartig tissue" and the fungus mantle are formed.—GEO. D. FULLER.

[21] MCDOUGALL, W. B., On the mycorhizas of forest trees. Amer. Jour. Bot. **1**:51–74. *pls. 4. fig. 1.* 1914.

[22] MELIN, ELIAS, On the mycorhizas of *Pinus silvestris* L. and *Picea Abies* Karst. A preliminary note. Jour. Ecol. **9**:254–257. 1922.

[23] RAYNER, M. C., Obligate symbiosis in *Calluna vulgaris*. Ann. Botany **29**:97–153. 1915.

Pigment development in Cyanophyceae.—BORESCH[24] finds that as cultures of *Phormidium Ritzii* var. *nigroviolacea* age the color gradually changes from the normal olive green, olive, or sepia brown, through violet, red violet, brown red, red brown, or even yellow brown. The addition of a small amount of iron salts leads to the return of the original color in a few days in diffuse light. These changes can be repeated in a given culture at pleasure. The author believes this is the first case of iron chlorosis reported for algae, although a number of cases have been reported in higher plants under practical growth conditions. In the young cultures there is much of a red violet water soluble protein pigment with a Venetian brown fluorescence along with much chlorophyll and carotin. As the color changes with iron deficiency, the carotin remains undiminished, but the other two pigments largely disappear.

The author states that it was known already that aside from species characters, the main conditions that have interested investigators in pigment development in the blue green algae are N-chlorosis, which is very likely to occur in ordinary cultures with aging, and the effects of intensity and quality of light. In monochromatic light there is a change in the quantity of phycocyanin, and in full sunlight there is a great diminution in the amount of both chlorophyll and phycocyanin.—WM. CROCKER.

Use of nutrient salts of low solubility.—The value of certain relatively insoluble salts as sources of necessary ions for the growth of seed plants has been tested by DUGGAR[25] in a variety of combinations, but by no means covering the entire range of possibility. It is argued that in certain types of work many advantages may accrue from the use of combinations of insoluble salts, because of the tendency to maintain a constant concentration of the various ions furnished, and also because no renewal of the solution (except as to addition of NO_3) is required from day to day. In each of three cultures in which wheat or wheat and corn were used, one or more of the combinations containing two or more insoluble salts exceeded the growth in the best control culture employed. Soluble ferric phosphate, and in certain cases ferric citrate, proved very valuable. The reason for the marked beneficial action of these is not yet determined. In most cases in these experiments the P_H lay between 5.6 and 8.0, and with growth the P_H shifted somewhat toward alkalinity.—WM. CROCKER.

Life history of a Pezizella.—SHEAR and DODGE[26] have uncovered an interesting life history of an Ascomycete, and have illustrated the present

[24] BORESCH, K., Ein neuer die Cyanophyceenfarbe bestimmender Faktor. Ber. Bot. Gesells. **38**:286–287. 1920.

[25] DUGGAR, B. M., The use of "insoluble" salts in balanced solutions for seed plants. Ann. Mo. Bot. Gard. **7**:307–327. 1920.

[26] SHEAR, C. L., and DODGE, B. O., The life history and identity of "*Patellina Fragariae*," "*Leptothyrium macrothecium*," and "*Peziza oenotherae*." Mycologia **13**: 135–170. *pls. 8–10.* 1921.

chaos in the taxonomy and morphology of this group, and the imperative need of a more stable system of nomenclature. A study of the life history of the Ascomycete to which they assign the name *Pezizella lythri* reveals the following facts. The life cycle includes three stages. The conidial stage has received at least seven generic and ten specific names; the pycnidial stage has been referred to at least four genera, and has had at least twelve specific names; while the ascogenous stage has been described but once so far as known. In one or another of its stages, this fungus has been found on about fifty different host plants, widely distributed throughout North America and Europe, and it also occurs in South America. With such a range of forms and hosts and geographical occurrence, it is not surprising that names multiplied, but intensive studies of life histories will bring some order out of such confusion.—J.M.C.

Rhus poisoning.—The nature of the poisonous principle in *Rhus* and the method of its transmission from plant to person has excited much controversy. There have been two main theories: (1) that the poison is volatile, and therefore infection can take place without contact with the plant, and (2) that the poison is non-volatile, contact with the plant being necessary for infection. McNAIR[27] reports the results of experiments which lead him to conclude that the poisonous principle is non-volatile. Poisoning without contact with the plant can occur only by contact with something, such as clothing, shoes, etc., which has the poison on it, or from the smoke of the burning plants, the soot of which seems to carry the poison. He finds that the poisonous principle is confined exclusively to the resinous sap of the resin canals. The literature of the subject is well summarized, the work of PFAFF, who concludes that the poison is a non-volatile skin irritant, being especially emphasized. PFAFF applies the name toxicondendrol oil to the poison.—S. V. EATON.

Inhibition by metabolic products.—CHAMBERS[28] finds that the hydrogen ion concentration of the culture medium is very important in cultures of *Bacillus coli*. There is a slight checking of growth at P_H 5.5, and an increasing intensity to lethal concentration between P_H 5.1 and 4.9. Inhibition begins on the alkaline end from P_H 7.0 and 7.6, depending upon age of culture and other factors. P_H 7.6 is comparable in inhibitory action with P_H 5.1. In an asparagin-$CaCO_3$ bouillon P_H 9.5 is not fatal. In cultures with the hydrogen ion concentration controlled, the maximum count was 3,750,000,000 bacteria to the cubic centimeter, contrasting with 281,000,000 in dextrose bouillon with the hydrogen ion uncontrolled. "The inhibitory action of the metabolic products of dextrose other than the hydrogen ions is only evident near the critical acid concentration."—WM. CROCKER.

[27] MCNAIR, JAMES B., The transmission of *Rhus* poison from plant to person. Amer. Jour. Bot. **8**:238–250. 1921.

[28] CHAMBERS, W. H., Studies in the physiology of the fungi. XI. Bacterial inhibition by metabolic products. Ann. Mo. Bot. Gard. **7**: 249–289. 1920.

GENERAL INDEX

Classified entries will be found under Contributors and Reviewers. New names and names of new genera, species, and varieties, are printed in **bold-face** type; synonyms in *italic*.

A

Addisonia 424
Adenodaphne 160
Aecidium brasiliense 67
African Labiatae 244
Aitken, R. D., work of 248
Alistilus 244
Alkali soils 247
Amaranthus, germination of 213
Angiopteris evecta, vascular anatomy of 161
Animal burrows an ecological factor 336
Annularia with Paleostachya fruit 326
Anthocyan pigments 500
Arber, E. A. N., "Devonian floras" 414
Arctic plants 243
Arthur, J. C. 58
Asphodelus, derivation of a maritime species 336

B

Babcock, E. B., work of 154
Bacteria, classification of the anaerobic 70; life cycles of 505
Bahama, endemics of 423
Bailey, I. W. 245
Baker, E. G., work of 159
Baphia 160
Belotia 160
Bergerstein, A., "Die Transpiration der Pflanzen" 239
Bhide, R. K., work of 246
Blomquist, H. L. 181
Boeshore, I., work of 335
Bonnayodes 160
Boresch, K., work of 507
Bouyoucos, G., work of 420
Bower, F. O., work of 245
Bowman, H. H. M., work of 335
Brassica, sterility in 110
Braun-Blanquet, J., work of 498
Brenner, W., work of 420
Brown, J. G. 332, 333
Brown, N. E., work of 244
Browne, Isabel M. P. 447
Buchholz, J. T. 249
Burns, W., work of 245
Butler, O., work of 424

C

Cabbage, Fusarium resistant 155
Carbon nutrition 333
Carothers, E. Eleanor, work of 80
Centropogon 160
Cerotelium, Fici 59; **minutum** 59
Chakradev, G. M., work of 245
Chamberlain, C. J. 331, 417, 503
Chambers, W. H., work of 508
Chatton, E., work of 330
Chromosomes, inheritance of 80
Cionothrix praelonga 61
Citrus diseases in Orient 244
Clark, H. W., "Lake Maxinkuckee" 242
Claussen, R. E., work of 154
Climate and vegetation 416
Coleosporium Ipomoeae 59
Colloidal hydration 334
Composition of plants, relation of nutritive elements to 246
Comptonella 160
Contributors: Arthur, J. C. 58; Bailey, I. W. 245; Blomquist, H. L. 181; Brown, J. G. 332, 333; Browne, Isabel M. P. 447; Buchholz, J. T. 249; Chamberlain, C. J. 331, 417, 503; Coulter, J. M. 159, 243, 335, 415, 424, 508; Coulter, M. C. 80, 154, 157; Cowles, H. C. 80, 246, 334, 335; Crocker, W. 420, 421, 424, 507, 508; Denny, F. E. 44; Eaton, S. V. 246, 247, 422, 508; Evans, Clytee R. 213; Fuller, G. D. 158, 245, 248, 331, 336, 412, 413, 415, 416, 420, 422, 424, 502, 506; Gardner, M. W. 469; Greaves, J. E. 161; Hall, E. H. 401; Harvey, LeR. H. 26; Heller, Hilda H. 70; Jones, L. H. 391; Kendrick, J. B. 409; Knudson, L. 1; Lupo, Patsy 486; McDougall, W. B. 200; Martin, G. W. 236, 329, 330; Noé, A. C. 414; Norton, J. F. 505; Randolph, L. F. 337; Rayner, M. Cheveley 226; Robbins, W. J. 376; Robertson, C. 148; Rose, J. N. 242; Round, Eda M. 326; Sandstrom, W. M. 287; Sears, P. B. 308, 425, 500; Shantz, H. L. 239; Shive, J. W. 391; Shull, C. A. 153, 247, 333, 334, 336, 419, 499; Spessard, E. A. 504; Stout, A. B. 110; Swingle, W. T. 244; Thone, F. 497; Trelease, W. 133; Walker, J. C. 155; Weiss, F. 496, 503; Willaman, J. J. 287; Woodard, J. 81
Corn endosperm, abnormal behavior in 157

Coulter, J. M. 159, 243, 335, 415, 424, 508
Coulter, M. C. 80, 154, 157
Cowles, H. C. 80, 246, 334, 335
Crocker, W. 420, 421, 507, 508
Ctenoderma cristatum 61
Cyanophyceae, pigment development in 507

D

Daniel, L., work of 336
Deccan vegetation 245
Dendrophyllanthus 160
Denny, F. E. 44
Depanthus 160
Desmella Gymnogrammes 61
Developmental selection 249
Devonian floras 414
Dicheirinia binata 61
Dickson, J. G., work of 246
Diels, L., work of 244
Dodge, B. O., work of 507
Duggar, B. M., work of 507
Dunn, Grace A., work of 421

E

East, E. M., work of 154, 157
Eaton, S. V. 246, 247, 422, 508
Ecology, schools of 497
Embryology of Angiosperms 424
Emerson, R. A., work of 158
Endophyllum, guttatum 66; pumilio 67; Wedelliae 67
Enochoria 160
Equisetum giganteum, anatomy of 447
Ericaceae, nitrogen fixation in 226
Evans, A. W., work of 243
Evans, Clytee R. 213
Everest, A. E., work of 501
Evermann, B. W., "Lake Maxinkuckee" 242

F

Feustel, H., work of 417
Fitting, H., work of 498
Flowers and insects 148
Forest, and prairie, tension zone between 246; geography of New Jersey 80; symbiosis 200
Forestry, British 415
Fruits, formulas for calculating number 44
Fucus, vertical distribution of 334
Fuller, G. D. 158, 245, 331, 336, 412, 413, 415, 416, 420, 422, 424, 502, 506
Fusarium resistant cabbage 155

G

Gail, F. W., work of 335
Gardner, M. W. 469
Germination, effect of temperature on 213; of orchid seeds 1
Gilman, J. C., work of 156
Gleason, H. A., work of 160
Goodspeed, T. H., work of 154
Greaves, J. E. 161
Gymnosperm leaves, anatomy and biology of 417

H

Hall, A. J., work of 501
Hall, E. H. 401
Hanson, C. O., work of 415
Harper, R. M., work of 80
Harter, L. L., work of 333, 422
Harvey, LeR. H. 26
Hayes, H. K., work of 154
Headley, F. B., work of 247
Heather, ecology of 502
Hedrick, U. P., "Sturtevant's notes on edible plants" 413
Heller, Hilda H. 70
Holloway, J. E., work of 504
Holm, T., work of 243
Hutchinson, J., work of 160
Hybrid species 154
Hydathodes, variation in 248
Hydrogen ion concentration of nutrient solutions, influence of wheat seedlings on 391
Hypoxylon, stroma and formation of perithecia 486

I

Inhibition by metabolic products 508
Insects and flowers 148
Ishikawa, M., work of 331

J

Jean, F. C., work of 246
Jones, L. H. 391
Jones, L. R., work of 155, 156
Jones, W. N., work of 502

K

Kendrick, J. B. 469
Knudson, L. 1
Kofoid, C. A., work of 329

L

Labiatae, African 244
Lake Maxinkuckee 242
Lars-Gunnar, R., work of 498
Leaves, anatomy and biology of gymnosperm 417
Lester-Garland, L. V., work of 160
Leucadendron, water relations of 248
Lichens, action of on glass 423; Japanese 160
Livingston, B. E., work of 416
Loeb, J., work of 496
Loftfield, J. V. G., work of 499

Löhnis, F., work of 505
Lowe, E. N., work of 422
Lupo, Patsy 486

M

Macbride, T. H., "North American slime-moulds" 415
MacDougal, D. T., work of 334
McDougall, W. B. 200; work of 506
McKay, B. M., work of 334
McNair, J. B., work of 508
Macoun, J. M., work of 243
Maize, cytology of chlorophyll types 337
Mally, W., work of 332
Maravalia 60; **pallida** 60
Martin, G. W. 236, 329, 330
Matisse, G., work of 419
Melin, E., work of 506
Mellor, Ethel, work of 423
Merismostigma 160
Michigan, pine formation 26
Micronesia, flora of 244
Milesia **Blechni** 61
Mississippi, plants of 422
Modilevski, J., work of 503
Montagueia 160
Moore, S. LeM., work of 159, 160
Mycorhiza of forest trees 506

N

Neottia Nidus-avis, cytology of 503
New Caledonia, plants of 159
New Jersey, forest geography of 80
Nitrogen, content in alfalfa 401; fixation by green plants 247; fixation in Ericaceae 226
Noack, K., work of 419, 500
Noé, A. C. 414
North American slime-moulds 415
Norton, J. F. 505
Nuclear division, new type of 330
Nutrient salts of low solubility 507

O

Olsen, C., work of 331
Onions, pink root of 332
Orchid seeds, nonsymbiotic germination 1
Orobanchaceae and Scrophulariaceae 335
Orthogenesis 282, 284

P

Palmgren, A., work of 498
Paracryphia 160
Pearce, K., work of 160
Pemberton, C. C., work of 424
Peperomia 133; **amphoricarpa** 138; arifolia 142; **astyla** 137; Bakerii 145; bracteata 138; campylotropa 137; claytonioides 138; cordulata 143; **cordulatiformis** 143; fugax 141; gracillima 138; hernandifolia 144; **Killipi** 143; macrandra 140; maculosa 146; mexicana 140; monticola 136; Muelleri 142; ovato-peltata 139; **Painteri** 136; **Parryana** 137; peltata 139; **peltilimba** 145; podocarpa 144; puberula 142; **schizandra** 137; schizostachya 138; sciaphila 139; scutellata 145; tecticola 142; **tenuimucronata** 137; Tuerckheimii 141; variegata 146
Peridiniales, unarmored 329
Perkins, Janet, work of 244
Permeability 336
Pezizella, life history of 507
Phakopsora, Crotonis 59; Vitis 59
Phanerocalyx 160
Pine formation, Michigan 26
Pink root of onions 332
Pinus, water relations of 248
Plant diseases, biochemistry of 287
Pool, R. J., work of 246
Porphyra, cytology of 331
Potassium and growth of plants 424
Potato wilts, transmission of 333
Prairie vegetation 158
Puccinia, antioquinensis 63; Arachavaletae 63; **corticola** 63; Eupatorii 63; Gouaniae 63; graminis, sporidial infection in 503; Heliconiae 63; (?) **ignava** 64; invaginata 65; purpurea 66; Ruelliae 66; Scleriae 66; Smilacis 66; Spegazzinii 66; Synedrellae 66; Triumfettae 66
Pucciniosira pallidula 67

R

Raber, O. L., work of 336
Randolph, L. F. 337
Ravenelia Indigoferae 61
Rayner, M. Cheveley 226; work of 502, 506
Rea, Margaret W., work of 248
Reed, H. S., work of 496
Regeneration, quantitative relations of 496
Reinking, O. A., work of 244
Rendle, A. B., work of 159
Respiration of thermophiles 419
Reviews: Arber's "Devonian floras" 414; Bergerstein's "Die Transpiration der Pflanzen" 230; Evermann and Clark's "Lake Maxinkuckee" 242; Hedrick's "Sturtevant's notes on edible plants" 413; Macbride's "North American slime-moulds" 415; Russell's "Soil conditions and plant growth" 153; Weaver's "Root development in grassland formation" 412
Rhizophidium polysiphoniae in the United States 236
Rhizopus, amylase of 422; nutrients for 421

Rhus poisoning 508
Riccardia 243
Robbins, W. J. 376
Robertson, C. 148
Romell, L. G., work of 336
Root, systems 412; cultivation of excised tips 376
Rose, J. N. 242
Round, Eda M. 326
Rübel, E., work of 498
Russell, E. J., "Soil conditions and plant growth" 153

S

Sabnis, T. S., work of 246
Salaciopsis 160
Salts and permeability to acids 420
Sampson, H. C., work of 159
Sandstrom, W. M. 287
Sax, K., work of 155
Scaphiophora 244
Schlecter, R., work of 244
Sclerotinia cinerea, effect on plums 287
Scofield, C. S., work of 247
Scrophulariaceae and Orobanchaceae 335
Sears, P. B. 308, 425, 500
Selection, developmental 249
Shantz, H. L. 239
Shear, C. L., work of 507
Shive, J. W. 391
Shreve, F., work of 416
Shull, C. A. 153, 247, 333, 334, 336, 419, 499
Siphocampylus 160
Smith, T. O., work of 424
Soil, alkaline 247; conditions and plant growth 153; influences of salts on bacterial activities 161; moisture 420; sulphur as a factor in fertility 81
Souèges, R., work of 424
Spessard, E. A. 504
Sprague, T. A., work of 160
Stelar morphology 245
Stem tips, cultivation of excised 376
Sterility in Brassica 110
Stomatal, regulation 499; variation 248
Stout, A. B. 110
Stumps, overgrowth of 424
Sturtevant's notes on edible plants 413
Sulphur, content in alfalfa 401; in soil fertility 81
Swezy, Olive, work of 329
Swingle, W. T. 244
Symbiosis in forest 200

T

Taraxacum, leaf variation, rejuvenescence, and senescence in 425; variations in cytology and gross morphology 308
Taubenhaus, J. J., work of 332
Taylor, N., work of 423
Temperature, effect on germination 213
Thermophiles, respiration of 419
Thone, F. 497
Tisdale, W. B., work of 155
Tmesipteris 504
Tomato mosaic, overwintering in 469
Tortugas, vegetation of 335
Transpiration of plants 239
Trelease, W. 133; work of 415
Trinidad, Uredinales in 58
Triurocodon 244
Tropalanthe 160
Tryphostemma 160

U

Uredinales in Trinidad 58
Uredo, Adenocalymmatis 67; Cherimoliae 67; Mandevillae 67; Phyllanthi 67; rubescens 67; sabiceicola 67
Uromyces, columbianus 62; jamaicensis 62; Wulffiae-stenoglossae 62
Urtica dioica, ecology of 331

V

Vegetation and climate 416

W

Wainio, E. A., work of 160
Walker, J. C. 155
Wann, F. B., work of 247
Waterhouse, W. L., work of 503
Weaver, J. E., "Root development in the grassland formation" 412; work of 246
Webber, H. J., work of 157
Weimer, J. L., work of 333
Weiss, F. 496, 503
Wheat seedlings, influence on hydrogen ion concentration 391
Wheldale, M., work of 501
Willaman, J. J. 287
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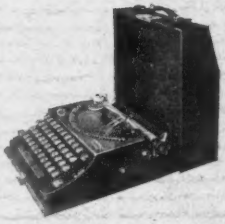

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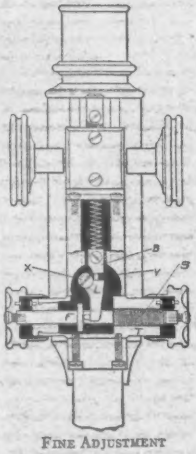

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